17

THE VICTORIAN ISOGRAPTIDS AND ISOGRAPTID-LIKE GRAPTOLOIDS

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ABSTRACT: The work of W. J. Harris on the Family Isograptidae Harris is reviewed, together with subsequent studies by others, notably Bulman and Skevington. A study is made of the proximal development, thecae, and rhabdosomal morphology of species included by Harris in the Family Isograptidae. The Family is reduced in status to a Sub-family, Isograptinae, in the Family Dichograptidae Lapworth. The genera *Oncograptus* and *Cardiograptus* are transferred to the Sub-family Cardiograptinae Mu and Zhan, and *Skiagraptus* to the Family Dichograptidae Lapworth. The status of *Maeandrograptus* is tentatively referred to the Family Sinograptidae Mu. The status of the numerous varieties of *Isograptus caduceus* is raised to the specific level.

The range of the isograptids in the Ordovician rocks of Victoria is considered and the retention of the term Isograptid Fauna is argued to be justified since the isograptids and isograptid-like species form an important unit in the Lower Ordovician rocks in Victoria.

The development and evolution of the isograptids is discussed and it is shown that while certain of the evolutionary trends postulated by Harris can be substantiated, others are found to be invalid on either, or both, palaeontological and stratigraphic evidence.

Finally, formal description of all the isograptid and isograptid-like species in Victoria are presented. In this section it is argued that *Isograptus caduceus* var. *victoriae* Harris and *Isograptus gibberulus* Nicholson are conspecific.

CONTENTS

INTRODUCTION ... *Page* 176
INTRODUCTORY NOTE ON ISOGRAPTID CLASSIFICATION ... 177
DEVELOPMENT OF THE PROXIMAL REGION IN ISOGRAPTIDS AND ISOGRAPTID-LIKE RHABDOSOMES ... 178
THECAL TYPES IN ISOGRAPTIDS ... 180
RHABDOSOMAL CHARACTERISTICS OF THE ISOGRAPTIDS ... 184
A REVISED CLASSIFICATION OF THE ISOGRAPTIDS ... 186
STRATIGRAPHIC ASPECTS OF THE ISOGRAPTIDS IN VICTORIA ... 188
DEVELOPMENT AND EVOLUTION OF THE ISOGRAPTIDS ... 188
SYSTEMATIC PALAEONTOLOGY ... 191
    Genus *Didymograptus* McCoy ... 191
    Genus *Skiagraptus* Harris ... 193
    Genus *Isograptus* Moberg ... 193
    Genus *Oncograptus* T. S. Hall ... 205
    Genus *Cardiograptus* Harris and Keble ... 208
    Genus *Pseudisograptus* Beavis ... 209
    Genus *Maeandrograptus* Moberg ... 212
CONCLUSIONS ... 212
REFERENCES ... 213

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INTRODUCTION

In 1933 W. J. Harris published his important work '*Isograptus caduceus* and its allies in Victoria.' He was aware of the limitations imposed on his work by the highly compressed state of preservation of the material available to him, and he anticipated a considerable revision of his ideas as more detailed studies on uncompressed material were completed. The results of Bulman's (1932b) work on Scandinavian graptolites were fully utilized by Harris and formed the basis for the major part of his taxonomic work.

On the basis of, particularly, the type of growth in the initial stages of the rhabdosome, Harris created a new family, the Isograptidae in which he included the genera *Isograptus* Moberg, *Maeandrograptus* Moberg, *Oncograptus* T. S. Hall, *Skiagraptus* Harris and *Cardiograptus* Harris and Keble. On the evidence available, Harris assumed that all species of these genera had the same type of proximal development as *Isograptus gibberulus*, determined for this species by Elles (1922), and defined by Bulman (1932a) as the Isograptid Type. Harris clearly believed, though he did not argue his case, that *Isograptus caduceus* and *Isograptus gibberulus* were conspecific.

Apart from the same type of proximal development, Harris considered that unity was given to the Family Isograptidae by progressive development along three lines (1933, pp. 85-86):

(i) the rhabdosome becomes increasingly scandent;
(ii) there is a progression, and then a regression, in the form of thecal apertures;
(iii) an increasing tendency towards concrescence 'which may be regarded as the chief basis for the Family.'

Harris could find no evidence to indicate the origin of the isograptids. However, he postulated three lines of development within the Family showing a number of evolutionary trends:

(i) A progressive increase in:
  (a) the size of the rhabdosome, with a more open spacing of thecae;
  (b) angle of divergence;
  (c) downward direction of denticles;
  (d) completeness of thecal overlap.
(ii) A development into allied genera marked by:
  (a) a reduction in size;
  (b) an increase in angle of divergence leading to dipleural biserial forms;
  (c) variation in denticles;
  (d) reduction in thecal overlap: the manubriate species;
  (e) grouping of thecal origins in the sicular region, as distinct from concrescence, but occurring with concrescence in *Oncograptus* and *Cardiograptus*.
(iii) The extinction of the Family except for rare forms.

The first revision of Harris's ideas came with the publication by Bulman (1936b) of evidence to show that the proximal development of *Oncograptus* was a dichograptid type, and much more primitive than that of any isograptid; he postulated derivation of *Oncograptus* from an ancestral *Tetragraptus*, independently of *Isograptus*. Mu and Lee (1958) agreed with Bulman's results, although later, Mu and Zhan (1966) claimed that Chinese material tended to support the original views of Harris on the development of *Oncograptus*.

In 1968, Skevington referred *Isograptus manubriatus* to the genus *Maeandrograptus*, which he included in the Family Sinograptidae Mu, largely on the basis of thecal morphology, notably the development of protheceal folds. He rejected as invalid the families Isograptidae Harris and Cardiograptidae Mu and Zhan. He regarded *Oncograptus* and *Cardiograptus morsus* as variants of his '*Maeandrograptus manubriatus*,' and *Skiagraptus* as a 'form genus' to which he referred *Cardiograptus crawfordi*. Bulman (1968) described the proximal development of an example of *Isograptus manubriatus* showing this to be a considerably modified isograptid type. In 1969, Whittington and Rickards described the proximal end of *Skiagraptus* showing this to be a modified dichograptid type, with an incipient monopleural arrangement of the thecae. This genus was referred by these workers to the Family Dichograptidae Lapworth.

Finally, Beavis (1972) discussed *Isograptus manubriatus* and showed that there is no justification for this species to be regarded as a maeandrograptid: at the same time, the species showed significant departures from the typical *Isograptus*, and a new genus *Pseudisograptus* Beavis was introduced to which were referred the three manubriate species: *I. manubriatus*, *I. hastatus*, and *I. dumosus*.

Since its publication in 1933, Harris's work has been subject to considerable revision, and this has been based particularly on proximal development of the rhabdosome. This present paper presents the results of the writers' research on this group of graptolites. Much of the work has been based on the compressed Victorian material, and preparation of the paper was deferred until the better preserved European and American material could be studied.

The final stages of the work, and the preparation of the paper were carried out at the Sedgwick Museum, University of Cambridge, during

a year's leave from the University of Melbourne. The work was undertaken at the suggestion of the late Dr. W. J. Harris. We are indebted to Professor O. M. B. Bulman for helpful discussion and criticism, to Professor H. B. Whittington for facilities, discussion and for his making available isolated specimens of *Skiagraptus* described by him and by Dr. R. B. Rickards. To Dr. Rickards and Professor Bulman we are indebted for their detailed criticism of the section of the work on the manubriate species.

In this paper, the following abbreviations are used— SM: Sedgwick Museum, University of Cambridge; NV: National Museum of Victoria; GV: Geological Survey of Victoria; GS: Geology School, University of Melbourne.

INTRODUCTORY NOTE ON ISOGRAPTID CLASSIFICATION

Although Harris accepted the ideas of Nicholson and Marr (1895) and of Elles (1898) that thecal characters are the most important criterion for familial separation, he appears to have regarded the type of proximal development of the rhabdosome as being of at least equal, if not greater, importance. He also accepted the conclusion of these earlier workers that such criteria as thecal spacing, thecal overlap, and apertural angle, were of genetic origin and of importance in generic distinction. Although he used these criteria, he pointed out that they are difficult, if not impossible, to distinguish in the Victorian material because of the compressed state of preservation.

Bulman (1963) discussed the basis for the classification of graptolites in general, showing that these organisms present two sets of separate characters: those of the rhabdosome as a whole, and those of the thecae. Changes in rhabdosomal form he indicated to be abrupt and irregular and taxonomic units based on these are precise and readily defined. The changes are astogenic, and taxa based on them may not be biologically valid. Bulman regarded thecal characters as a sounder basis for biological classification. In an earlier work (Bulman, 1955) he included the isograptids in the Family Dichograptidae, but in his 1963 paper, he remarked that 'some subdivision of this family has been proposed (e.g. Isograptidae Harris 1933, Sinograptidae Mu 1957) and is probably desirable at the Sub-family level.'

The Family Sinograptidae was introduced by Mu in 1957 to include some Chinese and European genera: *Allograptus* Mu, *Holmograptus* Kozlowski, *Tylograptus* Mu and *Sinograptus* Mu. This Family was extended by Jaanusson (1964) to include genera which do not necessarily have a dichograptid type proximal development but which were characterized by folding of the prothecae. The amended Family included *Meandrograptus* Moberg, *Oslograptus* Jaanusson and *Cymatograptus* Jaanusson in addition to the genera included by Mu.

Mu and Zhan (1966) proposed the Family Cardiograptidae to include the genera *Cardiograptus* Harris and Keble, *Paracardiograptus* Mu and Lee and *Skiagraptus* Harris. No formal diagnosis of the Family was published (at least in English), but the main characteristics are:

(i) the rhabdosome is two-stiped, usually with a well developed virgula;
(ii) the thecae have a dipleural arrangement;
(iii) the stipes are scandent.

In this paper (p. 186), a revised classification of the Victorian isograptids and isograptid-like forms is submitted. The original classification proposed by Harris was:

Order GRAPTOLOIDEA Lapworth 1875

Family DICHOGRAPTIDAE Lapworth 1873

Genus *Didymograptus* McCoy 1851
Didymograptus eocaduceus Harris
Didymograptus hemicyclus Harris

Family ISOGRAPTIDAE Harris 1933

Genus *Isograptus* Moberg 1892
Isograptus caduceus (Salter) et vars. Harris
Isograptus forcipiformis Ruedemann
Isograptus hastatus Harris
Isograptus manubriatus (T. S. Hall)
Isograptus dumosus Harris
Isograptus ovatus (T. S. Hall)

Genus *Oncograptus* T. S. Hall 1915
Oncograptus upsilon T. S. Hall
Oncograptus upsilon biangulatus Harris and Keble

Genus *Cardiograptus* Harris and Keble 1916
Cardiograptus morsus Harris and Keble
Cardiograptus crawfordi Harris

Genus *Skiagraptus* Harris 1933
Skiagraptus gnomonicus Harris and Keble

Genus *Maeandrograptus* Moberg 1892
Maeandrograptus aggestus Harris
Maeandrograptus tau Harris

Harris recognized the following varieties of *Isograptus caduceus: primula, lunata, victoriae* (forma typica), *maximus, maximodivergens, divergens, pertensa, imitata* and *tenuis.* The var. *horrida* is certainly a small form of *pertensa.* He considered two other possible varieties; *spinifer* and *expansa*, but concluded that they did not show sufficiently distinctive characters to warrant such recognition. All of these varieties were figured by Harris, but no formal descriptions were published.

DEVELOPMENT OF THE PROXIMAL REGION IN ISOGRAPTID AND ISOGRAPTID-LIKE RHABDOSOMES

At the time of the publication of his paper, Harris (1933) had available information on the proximal development of *Isograptus gibberulus* and *Maeandrograptus schmalenseei*. Since that time, details of the proximal development of *Oncograptus upsilon biangulatus* (Bulman, 1936b), *Isograptus manubriatus* (Bulman, 1968) *Maeandrograptus? geniculatus* (Skevington, 1965) and *Skiagraptus* sp. (Whittington and Rickards, 1969) have been determined from well preserved material. At the present time, information is available relating to the proximal development of at least one species of each genus included by Harris in the family Isograptidae, with the exception of *Cardiograptus*.

Isograptus gibberulus

The proximal development of this species was described by Elles (1898), Törnquist (1901), and Elles and Wood (1901). Elles (1922) apparently did not regard the development of this species as a distinct type, but she stated that *Isograptus gibberulus* 'showed the beginning of a structure characteristic of a more advanced type of development.' Bulman (1932a, 1932b, 1936a) formally defined the 'Isograptid type of development' in which th1^2, and not th1^1, was the dicalycal theca. *I. gibberulus* shows the '*gibberulus* stage of this type of development, with th2^1 developing somewhat lower down on th1^2 than in the more advanced *hirundo* stage, so that the crossing canal is more conspicuous.' Bulman (1932b) regarded the type of development as the most important characteristic, but he qualified this assertion by stating that since so little was known of other species of *Isograptus*, it remained uncertain as to which features were of generic importance.

In an isolated specimen from Killeröd, Sweden (SM No. A 513512) th1^1 arises very high up on the sicula (almost certainly the prosicula) and grows downward for its full length in contact with the sicula (Fig. 1a). Th1^2 arises about 0·6 mm below the bud of th1^1 (Fig. 1b). The second crossing canal is not clear in this specimen, but th2^1 appears to arise high up on th1^2.

The compressed Victorian material gives no evidence of the true nature of the proximal development, although in some examples (e.g. SM No. A 60286) the budding of th1^1 in the apical region of the sicula can be seen quite clearly. We must agree with Harris that, without the know-

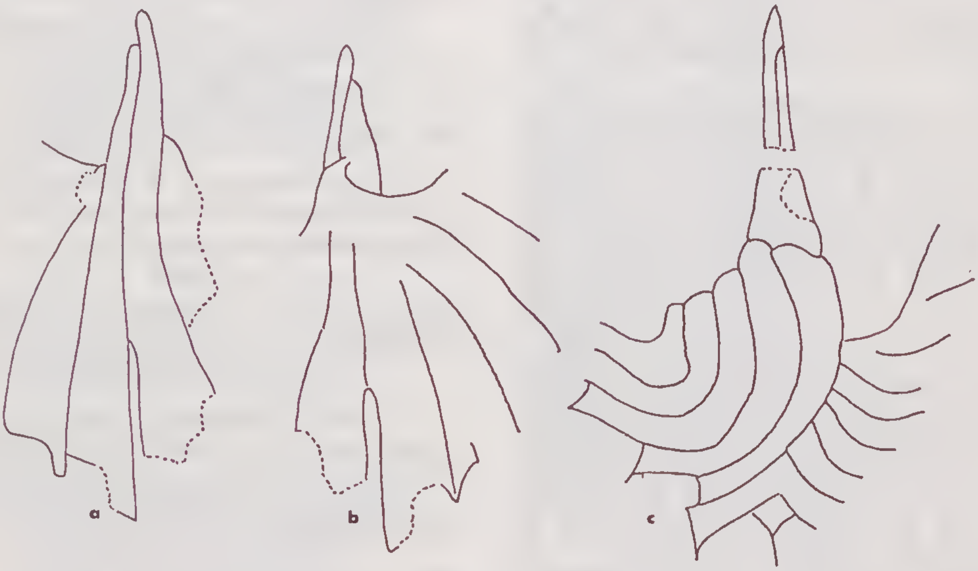


FIG. 1—(a) *Isograptus gibberulus* SM A513152 Lower *Didymograptus* Shales, Killeröd, Sweden, obverse aspect, × 12·5. (b) Same specimen as (a), reverse aspect, × 12·5. (c) *Pseudisograptus manubriatus* SM A603142 proximal end. Fort Pena Formation, Marathon, Texas, U.S.A. Latex mould, × 12·5, figured by Bulman (1968).

ledge from the uncompressed European material the data from the Victorian would be difficult, if not impossible, to interpret.

Pseudisograptus manubriatus

Harris implied that he did not understand fully the relationship between the manubriate, and the 'normal' species of *Isograptus*; he was prepared to assume, however, on the evidence available, that the proximal development of *'Isograptus' manubriatus* was isograptid, but of a special type. His figures 1a to 1e of Plate VI (1933) indicate that he was justified in his assumption, especially if he regarded as the main feature of the isograptid type of development that th1^2 was dicalycal, and this we believe he did. In 1968, Bulman described the development of a specimen of this species from Marathon, Texas (SM No. A 603142) which has been re-examined by the present writers. This species has, like other isograptids, a proximal development which is fundamentally platycalycal, i.e. th1^2 crosses th1^1 and the sicula by a crossing canal on the reverse side, leaving the sicula free on the obverse side. It does, however, simulate a pericalycal style in that the proximal portions of th4^1 to th6^1 seem to originate on the obverse side, and seem to cover, or enclose, some part of the sicula.

The sicula is long and narrow, and th1^1 buds high up on the sicula, but whether on the prosicula, as in *Isograptus gibberulus* is not clear. Th1^1 grows down along the sicula, and in contact with it until close to the apertural region, when it turns outwards. The origin of th1^2 is obscure, but it seems certain that this is the dicalycal theca giving rise to th2^1 and th2^2; th1^2 arises very low down on th1^1. One notable feature is the rapid proliferation of the th2^2 to th6^2 and the strong, but diminishing, semicircular curvature of these thecae (Fig. 1c). This type of development may be referred to as the isograptid (*manubriatus*) type: it is similar to the isograptid (*gibberulus*) type in as much as th1^1 arises high on the sicula, and grows in contact with the sicula for much of its length, in that th1^2 is the dicalycal theca, and the growth pattern is essentially platycalycal. It differs from the isograptid type in the simulation of a pericalycal growth pattern, and in the growth direction of the early thecae, particularly those of the secondary stipe.

Maeandrograptus

In his discussion of *Maeandrograptus schmalenseei* Bulman (1932b) noted that 'the structure of the proximal end of this genus is not quite so clear as in *Isograptus*, but seems to be essentially of the same type . . . th2^1 is derived from th1^2 (not th1^1) but it arises sooner in *Maeandrograptus* than it does in *Isograptus*—before the crossing canal of th1^2 has passed over the sicula. This is perhaps to be regarded as the more primitive condition.'

Skevington (1965) was able to determine the proximal development of *Maeandrograptus ? geniculatus* from isolated examples. The bud of th1^1 develops on the prosicula 0·2 mm below the apex; the theca grows down along the sicula for 0·4 mm where the foramen for th1^2 develops. Th1^1 continues its growth along the sicula to the apertural region of the latter, when it curves away from the sicula. Th1^2 completely obscures the sicula, on the reverse side, except for its proximal and apertural extremities. There is a pronounced curvature of th1^2, the aperture being directed away from the sicula. Th1^2 is dicalycal and gives rise to th2^1 and th2^2 at about the same level as in the isograptid (*hirundo*) type; th2^1 is, however, given off at the opposite side of the sicula from th2^2. Succeeding thecae bud off the preceding theca shortly after the origin of the latter.

In Victorian examples, proximal detail is never clear, but the curvature of the apertural regions of the earlier thecae away from the sicula can be seen. The *Maeandrograptus* type of development is quite similar to the isograptid type; that it is more primitive than the isograptid is open to conjecture: it is possibly a link between the isograptid (*gibberulus*) type and the manubriate type.

Oncograptus

Bulman (1936b) described and discussed his study of *Oncograptus* cf. *upsilon biangulatus* from Marathon, Texas (SM No. A 8140, A 8141). This material has been re-examined, but nothing new can be added to Bulman's conclusions. It has shown that th1^1 arises in the apical region of the sicula and grows down the sicula for about one half of its length, when it is separated from the sicula by the inter-position of another theca. Th1^2 is derived from th1^1 by a very broad crossing canal 'rather reminiscent of that of *Tetragraptus bigsbyi* but quite unlike that of *Isograptus gibberulus*'. From the base of the th1^2 the secondary stipe arises, but there is no second crossing canal. Th1^1 is the dicalycal theca, th2^1a and th2^1b arising from this. Th2^1a occupies the normal position on the primary stipe; th2^1b is very short, and grows round sharply on the side opposite the crossing canal, taking up a position between the sicula and th1^1, and opening between their apertures. The proximal development of *Isograptus* and *Oncograptus* are quite dissimilar, and Bulman regarded the two genera as totally unrelated.

Skiagraptus

Whittington and Rickards (1969) found the proximal development of *Skiagraptus* to be essentially dichograptid with an incipient monopleural arrangement of the thecae. $Th1^1$ is almost immediately formed and grows across the back of the sicula giving rise rapidly to $th2^2$, $th3^2$ . . . . Thecae subsequent to $th1^1$ and $th1^2$ became progressively shorter and more steeply inclined to the axis of the rhabdosome so that $th7^1$ is horizontally directed. In the early stages, when the thecae are growing downwards, each thecal tube crosses the axis of growth of the previous theca in the series. This seems to be the result of each initial bud attempting to grow at first dorsally to the previous theca and it is this which gives to the rhabdosome as a whole the incipient monopleural arrangement.

DISCUSSION

In erecting the Family Isograptidae, Harris assumed that all genera of the Family had the Isograptid (*gibberulus*) type of development. The results of the subsequent research, just summarized, show that this assumption was not valid for *Oncograptus* (and therefore presumably for *Cardiograptus* see Fig. 15j), *Pseudisograptus* or *Skiagraptus*.

The same type of proximal development, taken by Harris as one of the main taxonomic criteria at the familial level for the Isograptidae, does not in fact occur:

Isograptus caduceus
Isograptid (*gibberulus*) type

Pseudisograptus manubriatus
Manubriate type

Meandrograptus
Isograptid (*schmalenseei*) type

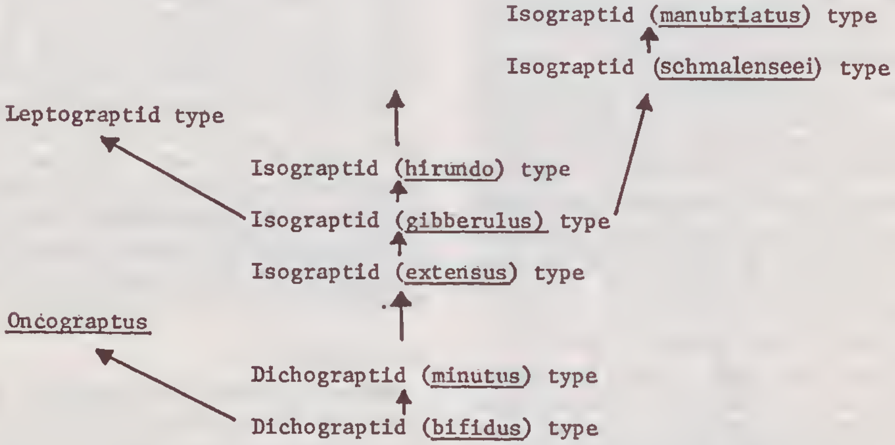
Oncograptus
Dichograptid type

Skiagraptus
Dichograptid type

Whether, in fact, the type of proximal development is taxonomically significant at this level is debatable, and will be considered later in this paper (p. 186). The types of proximal development are, however, related: a postulated relationship is shown in Table 1.

The isograptid (*schmalenseei*) type of development differs from the isograptid (*hirundo*) type in the growth direction of the apertural region of the early formed thecae. This is accentuated in the isograptid (*manubriatus*) type, in which, also, the marked curvature of the proximal thecae is distinctive. It would appear that the development of *Maeandrograptus* is slightly more advanced than that of *Isograptus gibberulus*, rather than being more primitive as suggested by Bulman (1932b). The budding positions of $th2^1$ and $th2^2$ on $th1^2$ in *Maeandrograptus* are similar to those shown in the isograptid (*hirundo*) type, which is a development from the *Isograptus* (*gibberulus*) type (Bulman, 1932b). In this paper (p. 188), stratigraphic evidence will be presented to support this idea. One important aspect which is emerging here is the close relationship of *Pseudisograptus* to *Maeandrograptus* and the intermediate position of the latter genus between the former, and *Isograptus*.

TABLE 1


Isograptid (manubriatus) type
Isograptid (schmalenseei) type
Leptograptid type
Isograptid (hirundo) type
Isograptid (gibberulus) type
Isograptid (extensus) type
Oncograptus
Dichograptid (minutus) type
Dichograptid (bifidus) type

THECAL TYPES IN ISOGRAPTIDS

Although Harris had available published descriptions and plates of thecae of *Isograptus gibberulus* and *Maeandrograptus schmalenseei* preserved in a more or less uncompressed state, he did not have the opportunity to examine such material, and all of his work was carried out on highly compressed and often poorly preserved specimens: it is remarkable that he was able to determine the amount of thecal detail which he has described. In this paper, thecal detail has been determined from the highly compressed Victorian specimens but in addition, uncompressed and isolated material from Europe and America was available for comparative purposes.

Isograptus caduceus AND RELATED SPECIES

Specimens of *'Didymograptus' caduceus* from the Skiddaw slates described by Elles (1898), and descriptions of Nicholson's types indicate that the thecae of *Isograptus caduceus* are simple tubes, in contact for almost their entire length. The proximal thecae are about 2 mm long and 0·7 mm wide. Distal thecae are much shorter (1·2 mm). Throughout the rhabdosome the thecae are remarkably uniform in general morpho-

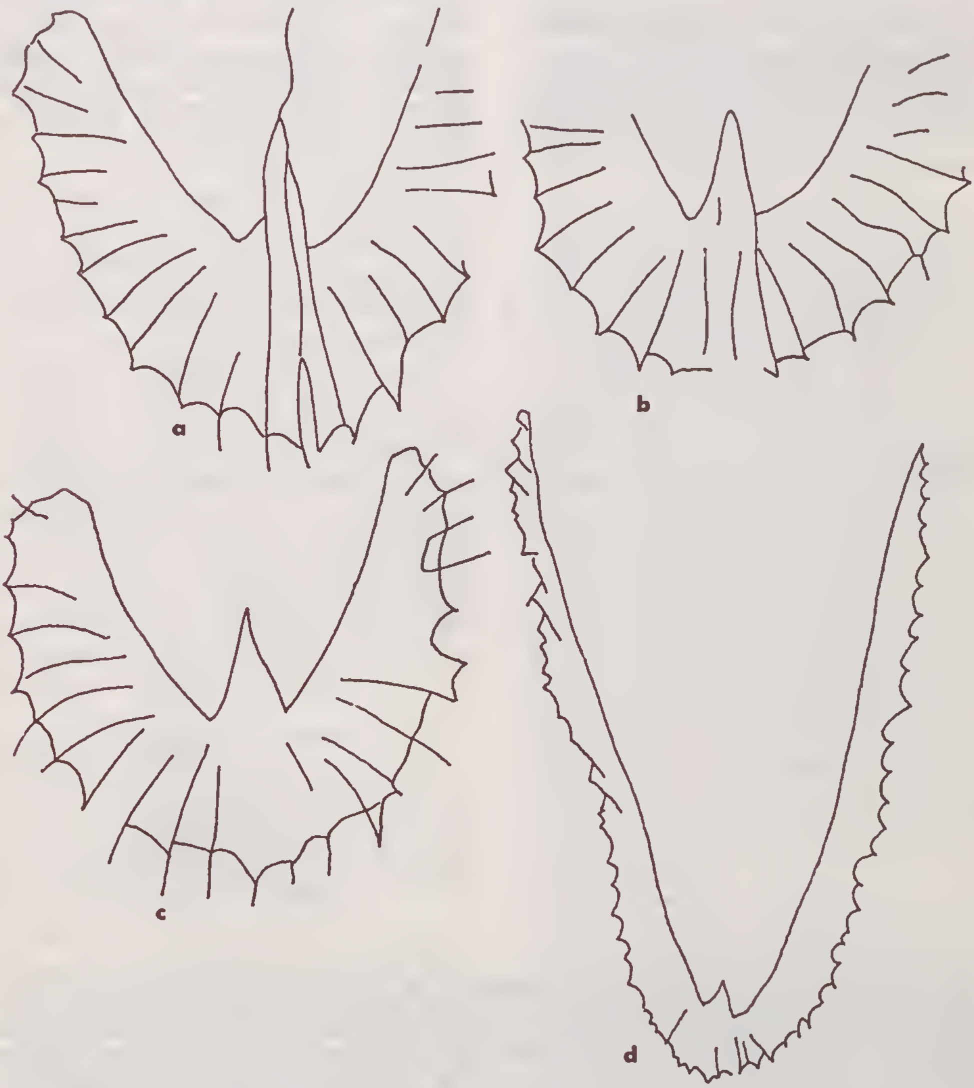


FIG. 2—a-c *Isograptus gibberulus* (? = *Isograptus victoriae*) Lower *Didymograptus* Shales, Killeröd, Sweden. (a) Obverse aspect SM A51315c, × 7·5. (b) Reverse aspect SM A51314b, × 7·5. (c) SM A51314a, × 7·5. (d) *'Didymograptus' caduceus* SM A17779 Syntype (Elles, 1901), figured Nicholson (1875). Skiddaw Crag, Skiddaw, England, × 3·75 approx.

logy and apertural characteristics. There is some slight variation in shape: all of the proximal thecae have a gentle curvature: in the distal thecae, the curvature is reduced, and some may be quite straight. Proximal thecae are pendent, the distal reclined, the change occurring gradually along the stipe. Thecal apertures are directed outwards (except for the proximal thecae, which have downward directed apertures) and are almost parallel to the stipe axis. Denticles are well developed and are almost normal to the apertural margins.

Bulman (1932b) did not give detailed descriptions of the thecae of *Isograptus gibberulus*, but his figures show that the thecae are virtually identical with those of *Isograptus caduceus*. Slightly compressed specimens of *Isograptus gibberulus* from Killeröd, Sweden (SM Nos. A51313, A 51314, A 51315) shown here as Fig. 2 a-c have all thecae, proximal and distal, slightly curved, while a single isolated specimen (SM No. A 513152) from the same area has the first theca, th1^1, straight, but other thecae are curved.

Most of the specimens figured by Harris (1933) as varieties of *Isograptus caduceus* have been destroyed, but examples of his var. *victoriae* from the type locality, Victoria Gully, Castlemaine, indicate that the thecae of this form accord closely in most if not all respects with those of forms described as *Isograptus gibberulus*. Cooper (1971, 1972) has published a note on *I. caduceus*. His general conclusions may be supported, but the

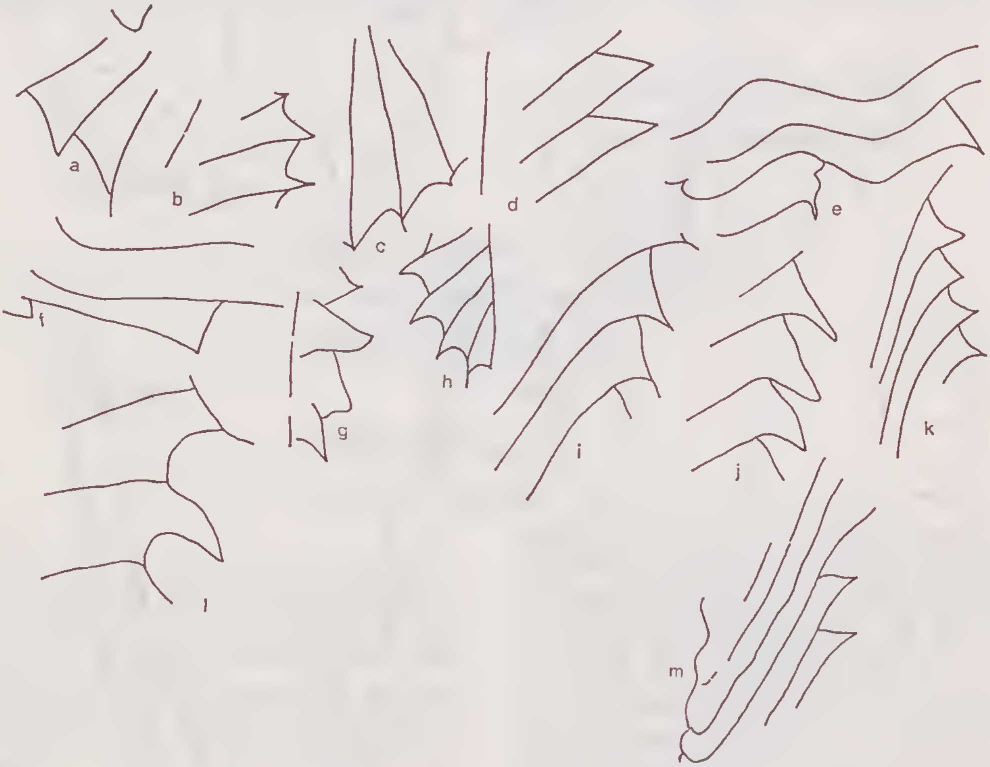


FIG. 3—Thecal types in Isograptids. All figures × 8 approx. (a) Proximal thecae of *Isograptus victoriae* SM A6320. Victoria Gully, Castlemaine, Victoria. (b) Distal thecae in same specimen as (a). (c) Proximal thecae of *I. gibberulus* SM A51315. Killeröd, Sweden. (d) Thecae of *Pseudisograptus manubriatus* SM A60283, Wileys Quarry, Macedon, Victoria. (e) Thecae of *Maeandrograptus schmalenseei* SM A23228 Lower *Didymograptus* Shales, Killeröd, Sweden. (f) Thecae of *Maeandrograptus tau* SM A6334 Loc. Ba71, Gisborne, Victoria. (g) Thecae of *Skiagraptus gnomonicus* SM A602856 Wileys Quarry, Macedon, Victoria. (h) Thecae of *Skiagraptus* sp. After Whittington and Rickards (1969). (i) Thecae of *Oncograptus upsilon biangulatus* SM A8141 Marathon, Texas. (j) Thecae of *Oncograptus upsilon* SM A22748 Loc. Ba71 Gisborne, Victoria. (k) Thecae of *Cardiograptus morsus* SM A6323c Chinamans Ck, Muckleford, Victoria. (l) Thecae of *Cardiograptus crawfordi* SM A60284 Strathfieldsaye, Victoria. (m) Thecae of *Pseudisograptus manubriatus* SM A603142 Marathon, Texas.

recognition of the varieties of Harris as subspecies of *I. victoriae* cannot be supported.

Pseudisograptus manubriatus

Harris (1933, p. 103) commented only briefly on the thecae of this species: 'The thecae number about 8 in 10 mm, resemble those of *Isograptus caduceus* in general form, but have rather less complete overlap, and a denticle which, though pronounced, is directed outwards rather than downwards, so that the thecal apertures open upwards rather than outwards. The apertural margin is also less concave.'

Skevington (1968) did not discuss thecal characters of this species in any great detail, but he noted that the 'tuft' of thecae at the level of the aperture of the sicula reflected the deflection of apertural portions of early formed thecae away from the sicula. Bulman (1968) observed that th1^2 to th6^2 all have a strong semi-circular curvature; subsequent thecae are relatively straight. Thecal curvature in the primary stipe is considerably less. Th1^1 is slightly curved, and curvature of thecae in this stipe decreases so rapidly that th6^1 is straight. The specimen described by Bulman (SM No. A 603142) shows th1^1 to th3^1 and th1^2 to th4^2 with downward directed denticles. In later thecae, the denticles are directed outwards, and the thecal apertures open upwards. Overlap is 0·75 to 0·80. The example shows thecal characteristics which differ markedly from those of *Isograptus*, the most important of which is the incipient prothecal folding. This although not strongly marked, is sufficiently developed to distinguish the thecae from the simple tubes of *Isograptus caduceus*.

Pseudisograptus hastatus, Pseudisograptus dumosus, Isograptus ovatus

For these species only the compressed Victorian material is available for study, and, as in the case of the Victorian specimens of *Pseudisograptus manubriatus*, thecal simplicity may be apparent rather than real.

The thecae of *Pseudisograptus hastatus* are conical tubes, 10 in 10 mm, overlapping by a little more than 0·5, and with a denticle much less pronounced than in *Isograptus caduceus*. The apertural margins are slightly concave, make an angle of up to 140° with the axis of the stipe, and open upwards. In *Pseudisograptus dumosus* the thecae are simple curved tubes. Proximally, overlap is almost complete, but distally, overlap decreases. The apertural margins are straight or slightly concave, and are directed more upwards than outwards. Harris noted (1933, p. 86) that there is a divergence from the 'typical trumpet shaped' thecae of *Isograptus caduceus*.

Isograptus ovatus has curved, expanding thecae, about 0·5 mm wide, and numbering 12 in 10 mm. Overlap is about 0·5. The apertural margins are usually deeply concave and the denticle is pronounced.

Isograptus forcipiformis

The thecae are strongly curved, and the width: length ratio (0·5) of the distal thecae is much greater than that of the proximal theca (0·20-0·24). The apertures are slightly to deeply concave, and tend to be directed outwards. Thecal overlap is almost complete. One interesting development noted in this form is an incipient monopleural arrangement of the thecae, so that there is a lateral, as well as a longitudinal overlap.

Maeandrograptus

Thecal characteristics of the Victorian species, *M. tau* and *M. aggestus* are almost impossible to determine. Harris noted for *Maeandrograptus tau* that the thecae have a low inclination, overlap is 0·3-0·5 increasing distally, and that the ventral margins are sigmoidally curved. For *Maeandrograptus aggestus* he was only able to note that 'the thecae are long tubes, circular or rectangular in cross section . . . apertures slightly concave and almost parallel to the axis of the sicula'.

Bulman (1932b) confirmed and enlarged on the earlier observations of Moberg (1892) and Törnquist (1901). The first two thecae on each stipe are shorter than the remainder, and overlap is considerably less. Later thecae increase greatly in length with an increase in overlap. The early thecae are flexed, but distal thecae, up to 7 mm long and 0·25 mm wide are almost straight. All of the thecae have a prominent denticle. Skevington (1965) drew attention to the prothecal folding, a feature absent from the thecae of *Isograptus*. At their origins, the interthecal septa bend into the prothecal folds.

Bulman (1969) commented on Skevington's work, noting that *Maeandrograptus ? geniculatus* has thecae closely resembling those of *Isograptus* in all respects other than the prothecal folds 'of a simple type'. Bulman appears to be hesitant to regard *Maeandrograptus* as being other than closely related to *Isograptus*, in spite of the differing thecae.

Oncograptus AND *Cardiograptus*

It is clear from uncompressed material (SM No. A 8140, A 8141 Bulman 1936b) that in the proximal region of the rhabdosome of *Oncograptus* there is a progressive deflection of thecal apertures away from the sicula. The apertural margins appear to be straight (although this is not always clear) and are directed outwards. Denticles are prominent and may be directed downwards or outwards. The thecae are relatively long, narrow tubes, with a strong sigmoidal curvature. Overlap is 0·8 to 0·9.

With only compressed specimens available, it is difficult to determine the thecal characteristics of *Cardiograptus*. They appear to be relatively simple tubes with a slight curvature. Apertural margins are straight to slightly concave, are directed downwards in the proximal thecae, and outwards in the distal thecae. The proximal thecae are strongly denticulate, but the distal thecae have less prominent denticles. Throughout, denticles are directed downwards.

Skiagraptus

In the type specimen of the Victorian *Skiagraptus gnomonicus* the proximal thecae grow along the sicula with their apertures opening downwards. The later thecae, apparently horizontal, have apertures directed downwards. Denticles are prominent. Whittington and Pickard (1969) described the thecae of *Skiagraptus* as simple, short and straight with a short dorsal process; the length of the distal thecae is much less than that of the proximal. Thecal apertures are rectangular.

ISOGRAPTID-LIKE DIDYMOGRAPTIDS: *Didymograptus eocaduceus* AND *D. hemicyclus*

These two species of *Didymograptus* have rhabdosomes which closely resemble *Isograptus*. In *D. eocaduceus* thecae are simple, slightly curved tubes, with overlap 0·50 to 0·65. The denticle is pronounced, and is directed outwards or slightly downwards. Apertural margins are concave and are directed upwards, making an angle of 100° to 125° with the stipe axis. In *D. hemicyclus* the thecae are long conical tubes, with overlap 0·30. The ventral and apertural margins are slightly curved. The denticle, often quite prominent, is directed outwards, or sometimes downwards.

DISCUSSION

One of the diagnostic characteristics of the Isograptidae defined by Harris was the simplicity ('*Didymograptus* type') of the thecae. *Isograptus caduceus* and its closely related species (the varieties of Harris), *I. forcipiformis* and *Oncograptus*, *Cardiograptus* and *Skiagraptus* all have such simple thecae. In *Maeandrograptus* and *Pseudisograptus*, however, the thecae are more complex types with prothecal, and in the proximal thecae of *Maeandrograptus schmalenseei* at least, longitudinal lateral wall folding. Moreover, the thecae lose the simplicity of those of the true *Isograptus*.

Apertural characteristics are surprisingly constant, although there is evidence that the apertures in *Maeandrograptus* and *Pseudisograptus* are more complex than in *Isograptus*. The suggestion of Harris that there is a progression, and then a regression in the apertural form of thecae of *I. caduceus* and closely related species is confirmed. Apart from this, no definite trends have been discerned.

RHABDOSOMAL CHARACTERISTICS OF THE ISOGRAPTIDS

The most obvious rhabdosomal feature of the isograptids is the reclined to scandent attitude of the stipes. All genera consist of two stipes: *Oncograptus* is proximally biserial, distally dividing into two uniserial stipes, while *Cardiograptus* and *Skiagraptus* are dipleural, and scandent throughout. The tendency towards a scandent growth direction and concrescence in the genera *Oncograptus*, *Cardiograptus*, and *Skiagraptus* was seen by Harris as one of the major evolutionary trends of the isograptids. There was some stratigraphic evidence to support this hypothesis: at least some of the evidence is not always convincing.

In this section, the rhabdosomal characteristics of the isograptids will be considered with special reference to size and spacing of thecae, angle of stipe divergence, and form of the proximal part of the rhabdosome, all of which have some taxonomic significance. The rhabdosomal (and thecal) characteristics are summarized in Table 2.

Isograptus gibberulus AND CLOSELY RELATED SPECIES

In the specimens of *Isograptus gibberulus* described by Bulman (1932b) the stipes are 2 cm long and decrease in width from 2·5 mm at their origin to 1 mm distally. Thecae number 10 to 16 in 10 mm. Proximally, the angle of divergence of the stipes is 270° but distally it is 320° to 330°. Proximally, the thecae grow almost parallel to the sicula.

Examples of '*Didymograptus*' *gibberulus* described by Elles (1898) from the Skiddaw slates have stipes 2 mm wide proximally, tapering to 1·0 to 1·25 mm distally. Angle of stipe divergence is 335° to 340°, and thecae number 16 in 10 mm. Elles distinguished three groups of varieties of *I. caduceus*, mainly on the basis of angle of divergence:

(i) dorsal walls of stipes continuously curved so that the distal extremities point towards each other;

Table 2

Thecal Characteristics

Rhabdosomal Characteristics

Species	Shape Proximal	Shape Distal	Length mm		Width mm		Growth Direction		Aperture	Direction of Denticle	Overlap %	No. of Stipes	Stipe Length cm	Stipe Width mm		Stipe shape	Divergence	Sicula Length mm	Thecae in 10 mm	Initial Growth	Remarks : Including direction of thecal apertures
			Prox.	Dist.	Prox.	Dist.	Prox.	Dist.						Prox.	Dist.						
Isograptus victoriae	Straight	Sigmoidal	2.0	1.2-1.5	0.6	0.6	Pendent	Scandent	Concave	Outwards	90	2	1.0+	2.5	2.0	Slight curvature	P250° D305-310°	4.5-5.0	11-12	'gibberulus'	Thecal apertures directed outwards. space between sicula and thl^1.
Isograptus gibberulus	Straight	Sigmoidal	2.0	1.3	0.7	0.5	Pendent	Scandent	Concave	Outwards	90	2	0.5	2.0	1.0	Curved	P180° D290-300°	4.5-5.0	13	'gibberulus'	space between sicula and thl^1.
Isograptus primulus	Straight	Straight	1.0	0.4	0.5		Pendent	Reclined	Slight Curvature	Downwards	80-90	2	0.5	2.0	1.0	Curved	P180° D290-300°	2.5	10-12	'gibberulus'	Stipes narrow rapidly.
Isograptus lunatus	Straight	Straight	1.0	0.6	1.0	0.6	Pendent	Reclined-Scandent	Concave	Downwards and Outwards	100	2	1.0	1.5+	1.0+	Straight	295-310°	3.0	11-14	'gibberulus'	Thecal apertures directed outwards or upwards
Isograptus maximus	Sl. curved	? Straight	2.5-4.0		0.7-0.8		Pendent	Scandent	Concave	Downwards	90+	2	1.5-2.0	2.0	2.0	Straight to Sl. curved	300-310°	5.5-6.0	10-11	'gibberulus'	Thecal apertures directed outwards.
Isograptus maximodivergens	Strongly curved	Curved	2.5-3.0	2.5-3.0	0.4	0.3±	Pendent	Reclined	Concave	Downwards and Outwards	90+	2	2.5-3.0	2.5	up to 4.0	Straight to Sl. curved	315-325°	2.5+	8-9	'gibberulus'	Very large specimens known. Thecal apertures directed outwards.
Isograptus divergens	Curved	Curved	4.0	4.5	2.0	2.5	Pendent	Reclined	Concave	Downwards	80-90	2	4.0	2.0	2.5	Straight-curved	330-335°	3.0	10-11	'gibberulus'	Thecal apertures directed outwards.
Isograptus imitatus	Straight-curved	Straight	1.5+	1.0±	0.5±	0.5±	Pendent	Reclined	Straight	Downwards	80-100	2	1.5	3.0	2.0-2.2	Straight	325-340°	2.5-5.0	8-10	'gibberulus'	Thecal curvature increases distally; apertures directed outwards.
Isograptus velatus	Straight-curved	Straight	1.5-2.0	0.9-1.1	0.6	0.5	Pendent	Reclined	Straight	Downwards	60	2	0.5	1.5-2.0	1.0	Slightly curved	330-340°	3.0	9-10	?'gibberulus'	Thecal apertures directed outwards for all thecae.
Isograptus tenuis	Straight	Straight	0.7	0.7	0.4	0.4	Pendent-Horizontal	Reclined	Straight	Outwards	30	2	0.6	0.6	0.6	Curved	300-305°	1.3+	12-14	?'gibberulus'	Stipes very slender. Thecal apertures directed outwards.
Isograptûs harrisi	Curved	Slightly curved	1.7	1.25	0.5	0.4-0.5	Pendent	Reclined	Concave	Outwards	85-100	2	0.3-0.x	1.8-2.0	0.8-0.9	Curved	P180°D330°	3.6	13-15	'gibberulus'	
Pseudisograptus manubriatus	Curved	Straight	2.0	4.0	0.7-1.0	1.0-	Pendent-Curved	Reclined	Concave	Outwards Upwards	60	2	1.0+	2.8±	3.0±	Straight	130-140°P 300°D	6-8	10	'manubriatus'	Initial growth modified Isograptid : 'platycalycal'. Thecal apertures directed upwards.
Pseudisograptus hastatus	Straight	Straight	1.0-1.5	1.0	0.4-0.5	0.4-0.5	Pendent-Curved	Reclined	Slightly Concave	Outwards	50-60	2	1.0	0.7	0.6	Tapering	330°	5.0-6.0	10-12	'manubriatus'	Thecal apertures directed upward except in sicular region.
Pseudisograptus dumosus	Curved	Curved	1.5	1.4±	0.4	0.45	Pendent-Curved	Reclined	Concave	Outwards	0.95P 0.70D	2	0.4±	1.0	0.7	Curved	330-360°	3.5+	8-9	'manubriatus'	Thecal apertures directed upward.
Isograptus ovatus	Curved	Curved	1.5	1.5	0.5	0.5	Pendent	Reclined	Concave	Outwards and Downwards	50	2	1.0	1.0	1.0	Curved	360°+ Dist.	3.0±	12	?'manubriatus'	Thecal apertures directed outwards.
Isograptus forcipiformis	Curved	Curved	1.2	1.0	0.5	0.4	Pendent	Reclined-Scandent	Concave	Downwards	100 -	2	0.7	4.0	1.0	Straight	360°	3.5-4.0	9-11	'gibberulus'	Thecal apertures directed outwards and upwards (distally).
Isograptus pertensus	Straight	Straight	4.0	1.5	0.7	0.7	Pendent	Scandent	Concave	Downwards-Outwards	95	2	6-8	3.0	1.5	Straight	340°	7.5	6-7	?'gibberulus'	Thecal apertures directed outwards.
Oncograptus upsilon	Curved	Sigmoidal	5.0	4.0	1.0	0.8	Pendent	Scandent	Concave	Downwards	90-100	Biserial Uniserial (2)				Straight	330°		12-13	Dichograptid	) Length of uniserial stipes varies widely. Thecal apertures))
Oncograptus upsilon biangulatus	Curved	Sigmoidal	5.0	4.0	1.0	0.8	Pendent	Scandent	Concave	Downwards	90-100	Biserial Uniserial (2)				Straight-curved	335-340°		12-13	Dichograptid	) directed outwards and upwards.
Cardiograptus morsus	Curved	Sigmoidal	3.0	6.0	?	0.9	Pendent	Reclined	Concave	Outwards and Downwards	95-100	Biserial							10	? Dichograptid	Thecal apertures directed outwards. Rhabdosome up to 2.0 cm. long.
Cardiograptus crawfordi	Curved	Slightly curved	2.0	2.6	0.6	0.5	Pendent	Scandent	Concave	Downwards and Outwards	100	Biserial							11-13	? Dichograptid	Thecal apertures directed outward.
Skiagraptus gnomonicus	Curved, short	Curved	1.0	1.5	0.5	0.5	Pendent	Scandent	Straight Concave	Downwards and Outwards		Biserial							12-13	Dichograptid	
Maeandrograptus tau	Sigmoidal	Sigmoidal	1.5		0.4		Horizontal	Horizontal	Concave	Downwards	33-50	2	0.5	1.0	0.8	Straight	180°+	2.5-5.5	9	Maeandrograptid	Modified Isograptid initial development.
Maeandrograptus aggestus	Sigmoidal	Straight?	1.2		0.3		Horizontal	Horizontal	Straight	Downwards	50(P)-100(D)	2				Straight	180°	2.5		Maeandrograptid	Modified Isograptid initial growth.

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(ii) dorsal walls straight, so that the stipes are parallel;

(iii) dorsal walls straight; distal extremities directed away from each other.

Isograptus victoriae (the var. *victoriae* of Harris) in Victoria has rhabdosomal characteristics which correspond closely with those of *I. gibberulus*. Distally the stipes diverge at 330° proximally; the angle of divergence is 260° to 290°. The form was described by Harris as 'horse-shoe shaped'. Stipes are 1·5 to 2·0 mm long, and narrow from a width of 2 mm proximally to 1·0 to 1·2 mm distally. Dorsal walls of the stipes have a slight curvature. Thecae number 10 to 15 in 10 mm.

Isograptus primulus, the first of the isograptids to appear in Victoria, has a small rhabdosome, with stipes consisting generally of only 2 or 3 thecae. The stipes are wide in the sicular region, but narrow rapidly. *I. lunatus* has the external form of *I. caduceus* except that the dorsal stipe walls are more strongly curved in the style of Elles' variety (i). The stipes are narrow, and have a uniform width. The dorsal stipe walls of *I. maximus* may be straight or slightly curved with an angle of divergence equal to, or slightly more than that of *I. caduceus*. The stipes maintain a uniform width throughout, but the dimensions may be as much as twice those of *I. caduceus*. An increase in the angle of divergence, and a narrowing of the stipes at the point of flexure characterize *I. maximo-divergens*. Stipes in this species may be 5 cm long and 5 mm wide. *I. divergens* is marked by the thinness of the stipes and a decrease in robustness of the rhabdosome.

Harris regarded *I. pertensus* as a variety of *I. caduceus* closely related to *I. divergens*, but Beavis and Beavis (1968) described it as a distinct species. In *I. pertensus* the stipes may reach a length of 10 cm. Angle of divergence is proximally 340°, and gradually the stipes become parallel. The sicular region is spinose and distally there are only 7 thecae in 10 mm. The var. *horrida* of Harris is identical with *I. pertensus* in every respect except size.

The stipes of *I. forcipiformis* are parallel to each other and are up to 2 cm long. Initially over 2 mm wide, the stipes taper until they are 1 mm or less in width. The narrow space between the dorsal walls of the two stipes is characteristic. *I. imitatus* varies considerably in size, but is otherwise close to *I. lunatus*. *I. tenuis* is an attenuated 'horse-shoe' shaped form with a thin periderm, while *I. velatus* has some characteristics of the manubriate isograptids. *I. ovatus*, also closely relatd to the manubriate species, has stipes of uniform width, about 1 mm, with the dorsal margins strongly curved. The stipes may reach a length of 1 cm. Angle of divergence varies, and the distal extremities of the stipes may be directed towards each other.

THE 'MANUBRIATE' SPECIES: *Pseudisograptus manubriatus*, *P. hastatus* AND *P. dumosus*

These forms have, apparently, a thickened sicular region. Hall (1914) ascribed this to a wide sicula; Harris, however, regarded it, correctly, as being due to the growth pattern of the first few thecae. In the species *P. manubriatus* the stipes vary in width from 2 to 3 mm and diverge initially at 300°. The thecae number 10 in 10 mm. Skevington (1968) examined this form in detail, and found an initial angle of divergence of 30°, later increasing to 130°-140° and ultimately to 300°. Beyond the sicular region, the stipes maintain a more or less uniform width.

P. hastatus has a small rhabdosome with stipes about 1 cm long, diverging ultimately at 330°. The stipes taper slightly. Thecae number 10 to 12 in 10 mm. The rhabdosome of *P. dumosus* is small, usually less than 5 mm in length. The dorsal walls of the stipes are strongly curved, but distally the dorsal walls are straight and the stipes are parallel to each other.

Oncograptus AND *Cardiograptus*

In *Oncograptus* the proximal region of the rhabdosome is biserial, but distally there is a bifurcation into two uniserial stipes. *O. upsilon* is 10 to 14 mm wide at the bifurcation, and the angle of divergence of the uniserial stipes is 320° to 330°. *O. upsilon biangulatus* is less than 10 mm wide at the bifurcation, with the uniserial stipes inclined at 330° to 340°. The uniserial stipes of *O. upsilon* are 5 mm wide; in *O. upsilon biangulatus* the width is invariably less than 5 mm.

Harris postulated (1933, p. 96) that 'the failure of *Oncograptus* to develop its uniserial stipes would result in a wholly biserial form. *Cardiograptus* is such a form'. In both known Victorian species of *Cardiograptus* the rhabdosome is 'heart shaped', but more so in *C. crawfordi* than in *C. morsus*. Two quite distinct forms of *C. morsus* occur: a broad form, and a narrow, but within each, the width varies between wide limits.

Maeandrograptus

The rhabdosome is small, each stipe being usually not more than 1 cm long. The sicula is long and slender, there is a slight tendency for a concentration of thecal origins in the sicular region. The distal thecae are excessively long, and have a very low inclination. The dorsal stipe walls are undulating, due to prothecal folding. Angle of divergence varies from 180° to 270°.

Skiagraptus

The rhabdosome of this genus is small: usually about 8 mm long, and 2 mm, or slightly less, wide. The thecal arrangement is dipleural, with an incipient monopleural development and the stipes are scandent, giving a biserial form. In the Victorian *S. gnomonicus* each stipe normally consists of about 8 thecae.

A REVISED CLASSIFICATION OF THE ISOGRAPTIDS

The formal diagnosis of the family Isograptidae Harris (1933, p. 100-101) reads:

> Biserial, initially biserial, or uniserial forms with stipes diverging at 180° or more, the proximal thecae growing at first entirely downwards and either opening in this direction or turning outwards, later thecae tending to become scandent. Thecae of the general type of *Didymograptus*.

Although he did not categorically assert that the isograptid type of development was the main basis for the Family, Harris implied this a number of times; he regarded also the direction of growth of the stipes as of major taxonomic importance. In classifying the isograptids the question of similar, or differing, thecal and rhabdosomal morphology is an important one: the relative significance of these at the several taxonomic levels is not always clear. It is, however, generally agreed that thecal characteristics are the most important in familial separation. On this basis, since, with the exception of *Maeandrograptus* and *Pseudisograptus* the thecae are didymograptid, the genus *Isograptus* must be regarded as a dichograptid, and the family defined by Harris reduced in status to a sub-familial level. At this level, it would seem that such criteria as angle of divergence and proximal development are significant, so that it is proposed to include here in the sub-family Isograptinae those species with a reclined growth direction and with the proximal development of the isograptid (*gibberulus*) type.

The sub-family Isograptinae (Harris) includes the single genus *Isograptus*. *Oncograptus* and *Cardiograptus* are included in the sub-family Cardiograptinae (Mu and Zhan). *Maeandrograptus* and *Pseudisograptus* have thecal characteristics of the sinograptids, and if thecal characteristics are to be the main criterion in familial distinction, then full familial status must be accorded to this group and not merely a sub-familial status as suggested by Bulman (1963). The inclusion of *Maeandrograptus* in the Family Sinograptidae Mu has been challenged by Bulman (1969). He states (p. 14):

TABLE 3

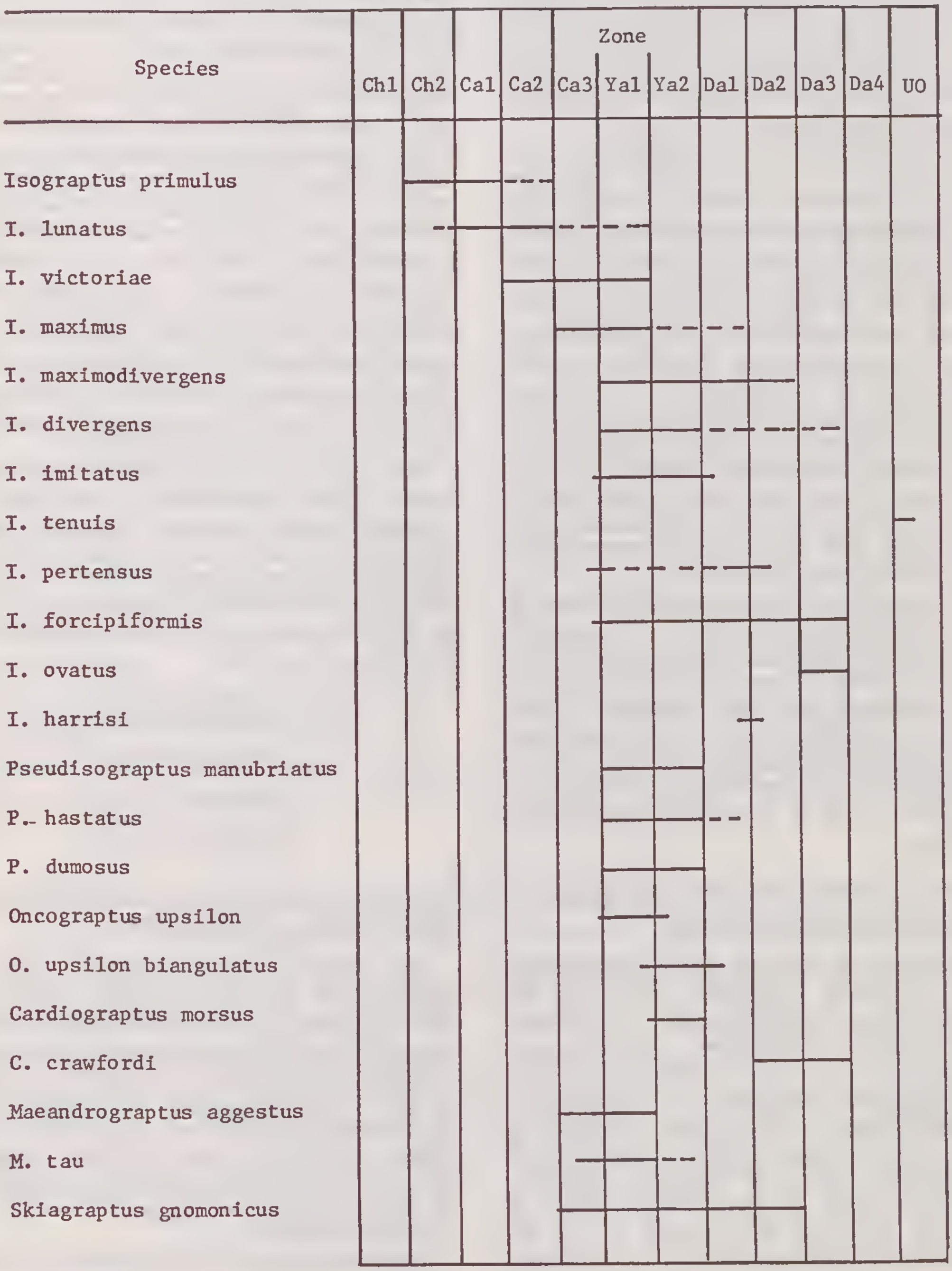
CLASSIFICATION OF THE VICTORIAN ISOGRAPTIDS

Order	GRAPTOLOIDEA Lapworth 1875
Sub-order	DIDYMOGRAPTINA Lapworth 1880 (amend)
Super-family	DICHOGRAPTACEA Lapworth 1873
Family	DICHOGRAPTIDAE Lapworth 1873
Genus	*Didymograptus* McCoy 1851 *Didymograptus eocaduceus* Harris *Didymograptus hemicyclus* Harris
Genus	*Skiagraptus* Harris 1933 *Skiagraptus gnomonicus* (Harris and Keble)
Sub-family	ISOGRAPTINAE (Harris) 1933
Genus	*Isograptus* Moberg 1892 *Isograptus victoriae* Harris *Isograptus primulus* Harris *Isograptus lunatus* Harris *Isograptus maximus* Harris *Isograptus maximodivergens* Harris *Isograptus divergens* Harris *Isograptus pertensus* Harris *Isograptus imitatus* Harris *Isograptus velatus* Harris *Isograptus tenuis* Harris *Isograptus ovatus* T. S. Hall *Isograptus harrisi* n. sp. *Isograptus forcipiformis* Ruedemann
Sub-family	CARDIOGRAPTINAE (Mu and Zhan) 1966
Genus	*Oncograptus* T. S. Hall 1914 *Oncograptus upsilon* T. S. Hall *Oncograptus upsilon biangulatus* Harris and Keble
Genus	*Cardiograptus* Harris and Keble 1916 *Cardiograptus morsus* Harris and Keble *Cardiograptus crawfordi* Harris
Family	SINOGRAPTIDAE Mu 1957
Genus	*Pseudisograptus* Beavis 1972 *Pseudisograptus manubriatus* (T. S. Hall) *Pseudisograptus hastatus* (Harris) *Pseudisograptus dumosus* (Harris)
Genus	*Maeandrograptus* Moberg 1892 *Maeandrograptus aggestus* Harris *Maeandrograptus tau* Harris

Unless overriding importance is attached to the presence of prothecal folding in the diagnosis of *Maeandrograptus*, it remains uncertain whether this genus is more closely related to a cymatograptid or to an isograptid. The very distinctive genotype *M. schmalenseei* has characteristics in common with both and the other species now being assigned to the genus extend its scope considerably by introducing new values.

Although Bulman argues convincingly, it is considered that *Maeandrograptus* should be referred, at least tentatively, to the Family Sinograptidae Mu. The reference of *Pseudisograptus* to this

TABLE 4
Stratigraphic Range of Species



Family is even more doubtful, but there is no question that while the thecal characteristics are not maeandrograptid (Beaves, 1972) they are certainly not dichograptid. On the evidence at present available, there seems to be no basis for regarding *Oncograptus* and *Cardiograptus* as sinograptids as suggested by Skevington (1968).

Skiagraptus has thecae of the general dichograptid type (Whittington and Rickards, 1969) although showing some departures from the simpler dichograptid thecae. The proximal development is of a modified dichograptid type, and on these grounds, this genus is referred to the Family Dichograptidae Lapworth.

In his paper, Harris (1933) discussed and figured a number of forms which he referred to as 'varieties' of *Isograptus caduceus*. On the basis of such criteria as thecal apertures, angle of divergence, and rhabdosomal morphology in general, these varieties are to be regarded as separate and distinct species of *Isograptus* and not as subspecies of *I. victoriae*. *Isograptus caduceus* var. *victoriae* was stated to be the '*forma typica*'. After the examination of a large number of examples of this form, and after comparison with European examples of *Isograptus gibberulus*, we are convinced these are conspecific; however, the Victorian form is here tentatively referred to as *Isograptus victoriae*. This form is certainly distinct from the form described by Cooper (1971, 1973) as *I. caduceus caduceus*.

The isograptid, and isograptid-like forms in Victoria comprise 25 species of 7 genera. In terms used by Australian geologists, *Didymograptus eocaduceus* and *D. hemicyclus*, are not part of the 'Isograptid Fauna'. The Isograptid Fauna ranges from the Chewtonian to the Darriwilian (from the *D. nitidus* subzone to the *D. hirundo*, or *D. bifidus* Zones, of Great Britain). *Didymograptus eocaduceus* and *D. hemicyclus* are Bendigonian species.

STRATIGRAPHIC ASPECTS OF THE ISOGRAPTIDS IN VICTORIA

For stratigraphic purposes it is highly desirable to retain the term 'Isograptid Fauna' for the genera *Isograptus*, *Pseudisograptus*, *Skiagraptus*, *Maeandrograptus*, *Cardiograptus* and *Oncograptus* as together they form a distinct bio-unit of great stratigraphic importance in Victoria. The stratigraphic range of each species is shown in Table 4. The stratigraphic value of the fauna is clearly demonstrated by the Table. In particular, the restricted range of many of the species is emphasized. The rapid development of the isograptids in the Castlemanian is also illustrated, and stratigraphic support for the contention of Harris that *I. primulus* → *I. lunatus* → *I. victoriae* → *I. maximus* → *I. maximodivergens* → *I. divergens* is obvious.

The isograptids appear first in the Chewtonian Ch2 Zone of *Didymograptus protobifidus* with *I. primulus* and, towards the top of the zone, *I. lunatus* enters. *I. primulus* is relatively short lived, but *I. lunatus* persists to the top of Ya1, although it is not common above Ca2. The isograptids have their maximum development in the Castlemanian and Yapeenian when they dominate the fauna, with a few didymograptids, phyllograptids, and rare tetrograptids occurring sporadically.

The Yapeenian is marked by the incoming of completely new forms: *Oncograptus* and *Cardiograptus*, and the appearance of *Pseudisograptus*. At the top of the Yapeenian, many of the isograptids become extinct, only a few species surviving into the Darriwilian, with only three new species appearing in the Darriwilian and one in the Upper Ordovician. The species *I. tenuis* is the only isograptid so far recorded from the Upper Ordovician, and it is known from only one locality. It is clear that the isograptids become totally extinct early in the Upper Ordovician.

With increasing knowledge of the Isograptid Fauna, a finer subdivision of the Castlemanian-Yapeenian may be possible. Ripper (1932) has suggested a subzone of *O. upsilon biangulatus*, while Harris and Thomas (1939) suggested the division of the Ya2 Zone into two subzones. Experience has shown that this suggestion is quite practicable in the field:

Subzone Ya2b
Oncograptus upsilon biangulatus
Cardiograptus morsus

Subzone Ya2a
Oncograptus upsilon
Cardiograptus morsus

DEVELOPMENT AND EVOLUTION OF THE ISOGRAPTID FAUNA

The evolution of the Isograptid Fauna is a problem, and the various workers involved have failed to agree on its solution. Harris used both palaeontological and stratigraphic data, and while there has been some quite strong criticism of some of his ideas, in particular those relating to the 'concrescent tendency' (e.g. Bulman 1936b, Skevington, 1968), as Thomas (1960) pointed out, 'Harris' general picture is logical, and because of its strong stratigraphic support it should not be dismissed too lightly'.

Isograptids appear quite suddenly in Victoria with the relatively simple *I. primulus.* Although reclined Isograptus-like species occur in the Bendigonian (*Didymograptus eocaduceus* and *D. hemicyclus*) there is no apparent connection between these and the isograptids.

As already noted, no doubt exists on either palaeontological or stratigraphical evidence that the isograptids developed in the sequence: *I. primulus* → *I. lunatus* → *I. victoriae* → *I. maximus* → *I. maximodivergens* → *I. divergens.* Harris claimed that this sequence showed four well marked trends:

(i) increase in size of the rhabdosome with a more open spacing of thecae;
(ii) increase in angle of divergence;
(iii) increasing downward-direction of denticles;
(iv) increasing thecal overlap.

Data relating to some of these trends are shown on Table 5.

Examination of the data, based on measurements of at least 30 specimens of each species, suggests that, even allowing for variations to be expected in biological systems, some of the 'trends' postulated by Harris are apparent rather than real. Thus, while there is no question regarding increase in size of the rhabdosome (expressed here in terms of stipe-length), or of increasing angle of divergence, the so called trends in thecal overlap and thecal spacing cannot be substantiated. In spite of this, there seems no doubt that these species represent a true evolutionary sequence, the palaeontological evidence in favour of the sequence being strongly supported by the stratigraphic evidence.

The main difficulties arise in some of the other postulates of Harris regarding the development of the isograptids:

(i) the 'manubriate tendency' with *I. maximus* giving rise to *P. manubriatus* and allied forms;
(ii) the 'concrescent tendency' along two lines from *I. divergens*:
    (a) giving rise to *Oncograptus* and thence *Cardiograptus*
    (b) giving rise to *I. tenuis, I. forcipiformis* and *Skiagraptus.*

These postulates have been criticized on palaeontological grounds. In fact, some of the stratigraphic data is also in error, and conclusions drawn therefrom are invalid. The most criticized postulate is that which derives *Oncograptus* (and *Cardiograptus*), from *Isograptus.* Bulman (1936b) expressed the view that *Oncograptus* was related to a tetragraptid. He showed quite convincingly that *Oncograptus* had no clear relationship with *Isograptus* and that it was 'derived from a tetragraptid in which the mode of development has not even progressed to the *minutus* stage of the dichograptid type . . . . It hardly seems probable that a proximal end with the structure of *Oncograptus* could progress further towards the diplograptid type of development, and hence that *Cardiograptus* . . . could be the ancestor of any "normal" diplograptid'.

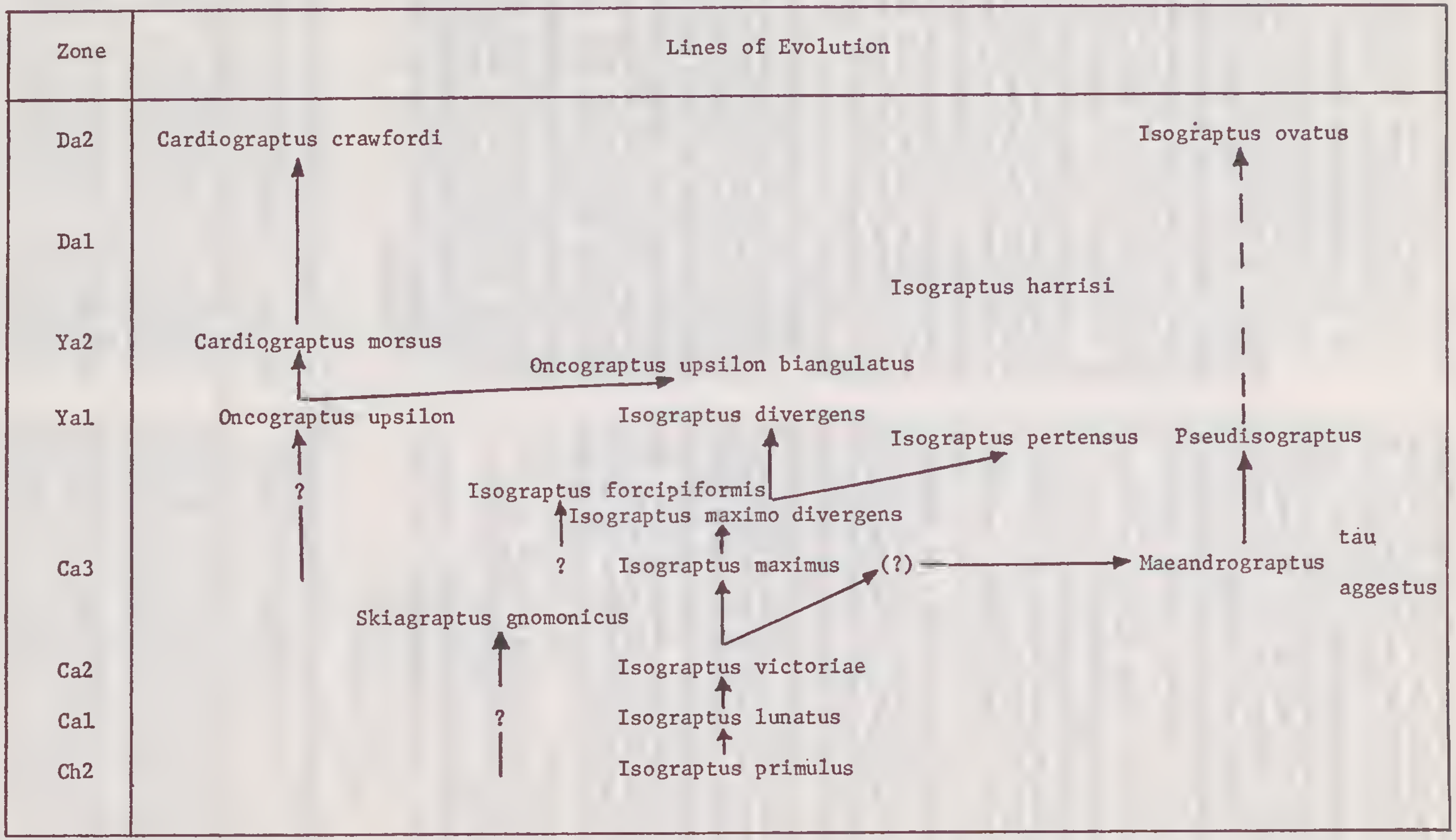
Bouĉek and Pribyl (1951) considered *Oncograptus* and *Cardiograptus* to have developed from *Isograptus*, which they derived from a tetragraptid ancestor. Thomas (1960) maintained (and he stated that Harris also held this view) that the isograptids are one of the links connecting the dichograptids with the diplograptids. *Isograptus* marks the stage at which th1^2 is dicalycal, and some of the later forms may have 3 crossing canals (although Thomas admitted this was not proved) and therefore follow the leptograptid type of development. He claimed two lines of development that became apparent:

(i) a concentration of crossing canals on the apical part of the sicula (the 'manubriate' species);

Table 5

Species	primulus	lunatus	victoriae	maximodivergens	divergens
Thecae in 10 mm	10–12	11–14	11–12	8–9	10–11
Thecal overlap	0.80–0.90	1.00	0.90	0 95	0.90
Divergence	290°–300°	295°–310°	305°–310°	315°–325°	300°–310°
Length of stripe	5 mm.	10 mm.	10 mm.	25–30 mm.	15–20 mm.

TABLE 6


Zone
Lines of Evolution
Da2
Da1
Ya2
Ya1
Ca3
Ca2
Ca1
Ch2
Cardiograptus crawfordi
Isograptus ovatus
Isograptus harrisi
Cardiograptus morsus
Oncograptus upsilon biangulatus
Oncograptus upsilon
Isograptus divergens
Isograptus pertensus
Pseudisograptus
?
Isograptus forcipiformis
Isograptus maximo divergens
tau
?
Isograptus maximus
(?)
Maeandrograptus
aggestus
Skiagraptus gnomonicus
Isograptus victoriae
?
Isograptus lunatus
Isograptus primulus

(ii) a concentration of crossing canals on the apertural part of the sicula (e.g. *Maeandrograptus*).

Thomas suggested that the former is one line of ascent of scandent forms, and the latter to the leptograptids. *Oncograptus* and *Cardiograptus* are on a side branch which, perhaps by retrogression soon become extinct. There seems to be little or no evidence to support this hypothesis.

Mu and Zhan (1966) stated that *Cardiograptus* is derived from *Oncograptus* (a point which has never been disputed) and that the Chinese material supports Harris' ideas on the origin of *Oncograptus*. Their statement, however, is of little value since they present no evidence of any kind.

The origins of *Skiagraptus* are unknown: it is a dichograptid, and its ancestry must be sought in more primitive dichograptids. It certainly did not originate from *Isograptus forcipiformis*, although having an incipient monopleural arrangement of thecae, and it lacks an isograptid type of proximal development. *I. forcipiformis* appears first high in the Ca3 zone, after *Skiagraptus* which appears first in the Ca2.

The palaeontological evidence supports the idea that *Pseudisograptus* evolved from *Maeandrograptus*: thecal types are similar, and there is an advance in the type of proximal development. There is probably a link between the isograptid (*gibberulus*) type of *I. caduceus* and the isograptid (*schmalenseei*) type of *Maeandrograptus* with the isograptid (*hirundo*) type development, but this has not been found yet in Victoria.

The postulated evolutionary relationships of the Isograptid Fauna in Victoria are shown in Table 6. In summary, it may be stated, that, while *Oncograptus* is almost certainly derived from a tetragraptid ancestor, there is no satisfactory evidence pointing to the ancestry of *Skiagraptus*.

SYSTEMATIC PALAEONTOLOGY

All of the forms included by Harris in his Family Isograptidae are described and figured in this section of the paper, together with several superficially similar but unrelated species. It would have been desirable in preparing the diagnoses of the species to have referred to the holotypes: where possible this has been done, but since most of Harris' figured specimens were accidentally destroyed by fire, in the majority of cases lectotypes have been selected. These, with one or two exceptions are lodged in the Sedgwick Museum, Cambridge. In every case, descriptions have been based solely on Victorian material: relevant comparative notes on American, European and British examples have, however, been included.

Order Graptoloidea Lapworth 1875
Sub-order Didymograptina Lapworth 1880 (emend)
Super-family Dichograptacea Lapworth 1873
Family Dichograptidae 1873
Genus **Didymograptus** McCoy 1851
Didymograptus eocaduceus Harris 1933

(Fig. 4a, b)

1933 *Didymograptus eocaduceus* Harris

Material: Lectotype NV No. 13800. Figured Harris 1933 Plate VI Figure 8A, Fig. 4a this paper. Other material examined: 33 specimens in GS collection. Preserved as limonite film on fawn slate.

Horizon and Locality: Bendigonian Zone Be1-2. Known only from Allot. 16, Parish of Campbelltown, Victoria.

Diagnosis: *Didymograptus* with stipes diverging initially at 180°, then becoming parallel, or convergent distally. Thecae simple cylindrical tubes, with concave apertural margins.

Description: The sicula is 1·5 mm long and about 0·5 mm wide at the aperture. The stipes vary in length from 0·5 cm to 1 cm, although one specimen with stipes 1·4 cm long was noted. Proximally the stipes are 0·8 mm wide, and narrow to 0·6 mm at the second or third thecae. They then widen to 1·0 mm and maintain this width for the remainder of their length. Initially the angle of divergence is 180° but at about the third thecae on each stipe, divergence increases so that the stipes are parallel, or in some cases converge.

Thecae are simple straight or curved tubes, 2 mm long and 1 mm wide. The apertural margins are usually straight, and they may be slightly concave; they are directed upwards, and make an angle of 95° to 135° with the axis of the stipe. Thecal spacing is constant with 11-12 thecae in 10 mm. Overlap is 0·5.

Remarks: Superficially this form resembles *Isograptus victoriae*. However, proximal development is clearly a simple dichograptid type. The thecae have much less overlap, the apertural margins are straighter, and are differently directed. The denticle, though pronounced, is less prominent than in *Isograptus*. This form is unrelated to *Isograptus*: it occurs in an isolated fauna notable for the number of species unique to it. It is probable that it developed from a reclined tetragraptid ancestor, by a failure of dichotomy.

Didymograptus hemicyclus Harris 1933

(Fig. 4c, d)

1933 *Didymograptus hemicyclus* n. sp. Harris

Material: Lectotype NV No. 13797. Figured Harris (1933) Plate VI Figure 4. Fig. 4c of this paper. Other material examined: 21 specimens GS collection. All material limonite films on fawn slate.

Horizon and Localities: Lower Bendigonian Be2. Known only from Allot. 16, Parish of Campbelltown, Victoria.

DIAGNOSIS: *Didymograptus* with narrow stipes having a semicircular curvature; initial angle of divergence 170°-180°, distally 260°-320°. Thecae simple conical tubes, apertural margins concave.

DESCRIPTION: The small sicula is 1 mm or slightly less long, and about 0·3 mm wide at the aperture. The stipes have a characteristic semicircular curvature, are rarely more than 5 mm long. Proximally the stipes

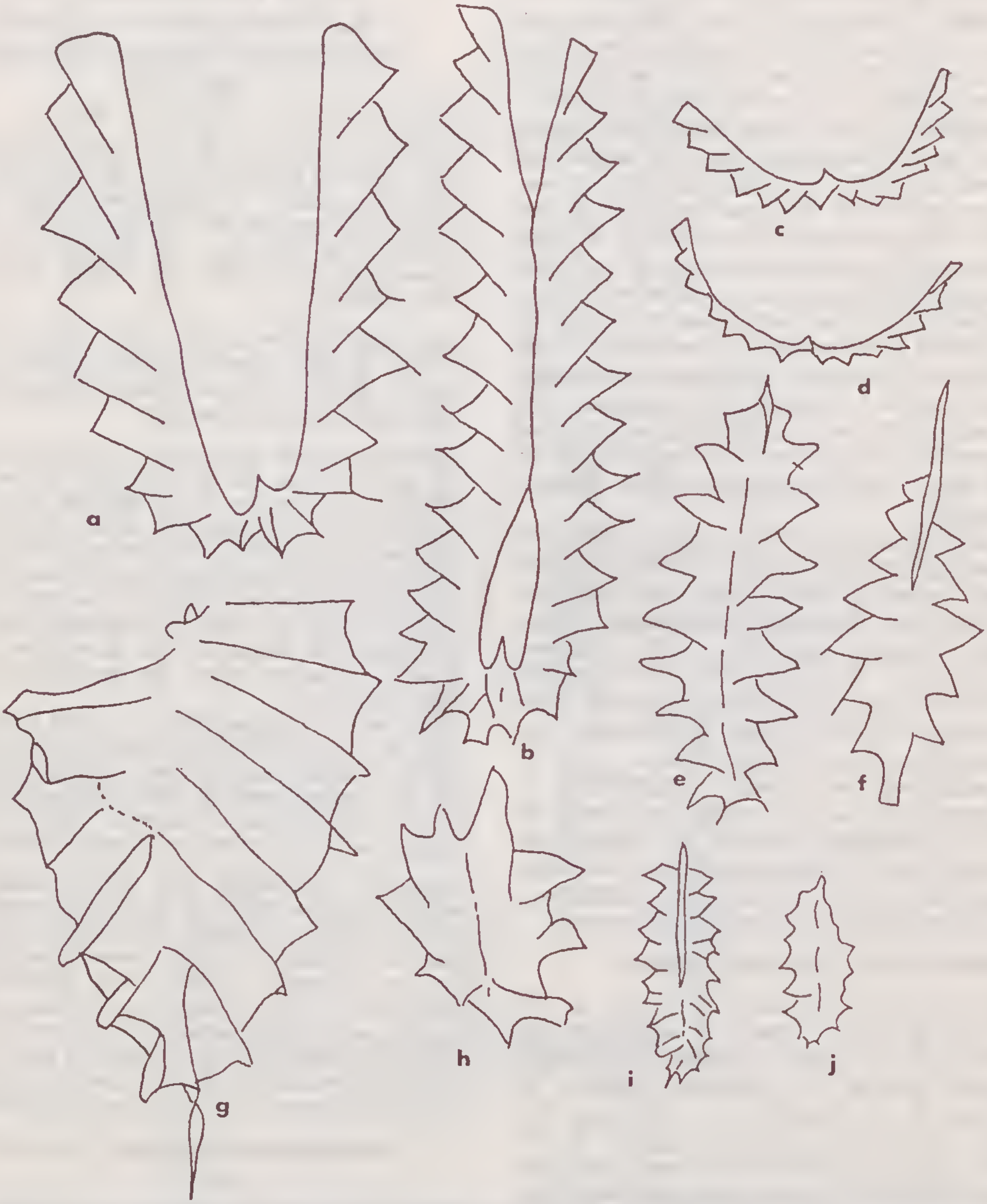


FIG. 4—*Didymograptus eocaduceus* (a) NV 13800 Lectotype. Allot. 16, Campbelltown, Victoria, × 7·5. (b) GS 3682. Same locality as (a), × 7·5. *Didymograptus hemicyclus* (c) NV 13797 Lectotype. Same locality as (a), × 3·75. (d) GS 3706. Same locality as (a), × 3·75. *Skiagraptus gnomonicus* (e) SM A6338 Lectotype. Loc. Ba71, Gisborne, Victoria, × 7·5. (f) SM A60285b Wileys Quarry, Macedon, Victoria, × 7·5, figured Skevington (1968). *Skiagraptus* sp. (g) Daniels Harbour, Newfoundland, × 31 approx., figured Whittington and Rickards (1969). *Skiagraptus gnomonicus* (h) GS 4000 Anakie Gorge, Victoria, × 7·5. (i) GS 4001 Little River Gorge, Brisbane Ranges, Victoria, × 3·75. (j) GS 4002 Moorabool River, Sheoaks, Victoria, × 3·75.

are 0·6 to 0·8 mm wide, distally 0·9 to 1·0 mm. Thecae are conical tubes with straight or slightly curved (concave downwards) ventral walls. Apertural margins are straight or slightly concave, and make an angle of a little more than 90° with the stipe axis. Thecal overlap is very low, it may be 0·1 and is never more than 0·35.

REMARKS: One of the more interesting aspects of this species is the nature of the thecae which are almost identical with those of *Didymograptus cuspidatus*, a form occurring very high in the Victorian sequence (Da3 Zone of *Diplograptus decoratus*). It has some resemblance to *Isograptus tenuis* notably in the curvature of the stipes and the general fragility of the rhabdosome. The thecae, however, are distinctly different.

Genus **Skiagraptus** Harris 1933

Skiagraptus gnomonicus (Harris and Keble) 1916

(Fig. 4e, f)

1916 *Diplograptus gnomonicus* n. sp. Harris and Keble in Harris (1933).
1924 *Diplograptus gnomonicus* H. and K. in Harris.
1933 *Skiagraptus gnomonicus* (H. and K.) Harris.

MATERIAL: The holotype cannot be located in any of the Victorian collections. Specimen SM No. A 6338 from locality Ba71, Gisborne, Victoria, is designated the lectotype and is figured here as Fig. 4c. SM No. A 60285b, figured Skevington (1968) from Wileys Quarry, Macedon, is figured as Figure 4f. Three other specimens GS 4000, 4001, 4002 have been examined and are figured (4h, i, j). Preserved as thin films on slate.

HORIZON AND LOCALITIES: This species has a long stratigraphic range, appearing at the top of the Castlemainian Ca2 and persisting to the top of the Darrwilian Da2. It has been recorded from Lancefield, Gisborne, the Castlemaine district, Brisbane Ranges and Macedon.

DIAGNOSIS: Rhabdosome scandent, biserial, dipleural, incipiently monopleural. Thecae short, distal thecae highly inclined, spacing 12-13 in 10 mm, overlap 0·8 to 0·9. Proximal thecae grow downwards, succeeding thecae horizontal, distal thecae reclined. Thecal apertures concave to convex. Proximal development, apparently dichograptid.

DESCRIPTION: The rhabdosome is small: usually 0·8 to 1·0 cm long and 2 mm wide. The sicula seems to be very short. A long virgula is invariably present, and this, in some cases, may be relatively thick. Thecae short, up to 2 mm wide, although usually slightly less; apertural margins are concave to convex, and are directed outwards. The prominent sharp denticles are directed downwards, although some are directed outwards.

REMARKS: Harris related this species to *Isograptus forcipiformis* deriving it from the latter by a continuation, and completion, of the 'concrescent tendency'. If *I. forcipiformis* is a true isograptid, and the evidence clearly demonstrates that it is, then such a relationship cannot exist. Apart from the difference in proximal development, there is a marked difference both in the types of thecae, and thecal growth patterns. Moreover, as already noted, the stratigraphic relationship precludes any possibility of development of *S. gnomonicus* from *I. forcipiformis*.

Sub-family ISOGRAPTINAE (Harris) 1933

REVISED DIAGNOSIS: Rhabdosomes of two uniserial stipes diverging at more than 180°, the proximal thecae growing entirely downward and opening in this direction; later thecae reclined. Thecae of the *Didymograptus* type. Proximal development Isograptid (*gibberulus*) type.

Genus **Isograptus** Moberg 1892

TRANSLATION OF ORIGINAL DIAGNOSIS (from Bulman, 1932b): 'Two branched rhabdosome, both branches of which grow out bilaterally symmetrical from the sicula. Each branch considered by itself is not bilaterally symmertically formed. The two impressions which one of these graptolites leaves on a shale surface and its counterpart always show in the matter of the proximal end (including the sicula) a somewhat different appearance. One can therefore distinguish a front and a back, and consequently also a right and a left branch'.

AMENDMENT OF DIAGNOSIS (Bulman, 1932b): 'One of the most important characteristics of this genus is the fact that the first stipe develops not from $th1^1$ as in the Dichograptidae in general, but from $th1^2$ *via* a second crossing canal. The first few thecae of both stipes grow entirely downwards, and the stipes, which are of considerable width at their origin taper gradually to their distal extremity'.

NOTE BY HARRIS (1933): 'The genus is here enlarged to include forms which are almost certainly related to *I. gibberulus* . . . The crucial test is probably the origin of the first stipe from $th1^2$ instead of $th1^1$ . . . Bulman's 'gradual tapering of the stipes' is almost certainly not of generic importance'.

REVISED DIAGNOSIS (Beavis, 1972): Rhabdosome didymograptid. Stipes reclined, angle of divergence always greater than 180°. Proximal development isograptid (*gibberulus*) type. Initial thecae straight, entirely pendent, later thecae reclined. Thecae of *Didymograptus* type, simple tubes, curved or straight.

REMARKS: The tapering of stipes, specifically mentioned by Bulman in his diagnosis is not, as Harris stated, of generic importance. Since tapering of stipes is probably a reflection of the differing growth direction of the thecae in the distal part of the stipe, it may be that the tapering is significant at the specific level. The initial development of the rhabdosome is of generic importance, and Harris' view that this is the 'crucial test' of the genus is quite valid.

Isograptus victoriae Harris 1933

(Fig. 5a-u)

1933 *Isograptus caduceus* var. *victoriae* Harris
1971 *Isograptus victoriae victoriae* Cooper

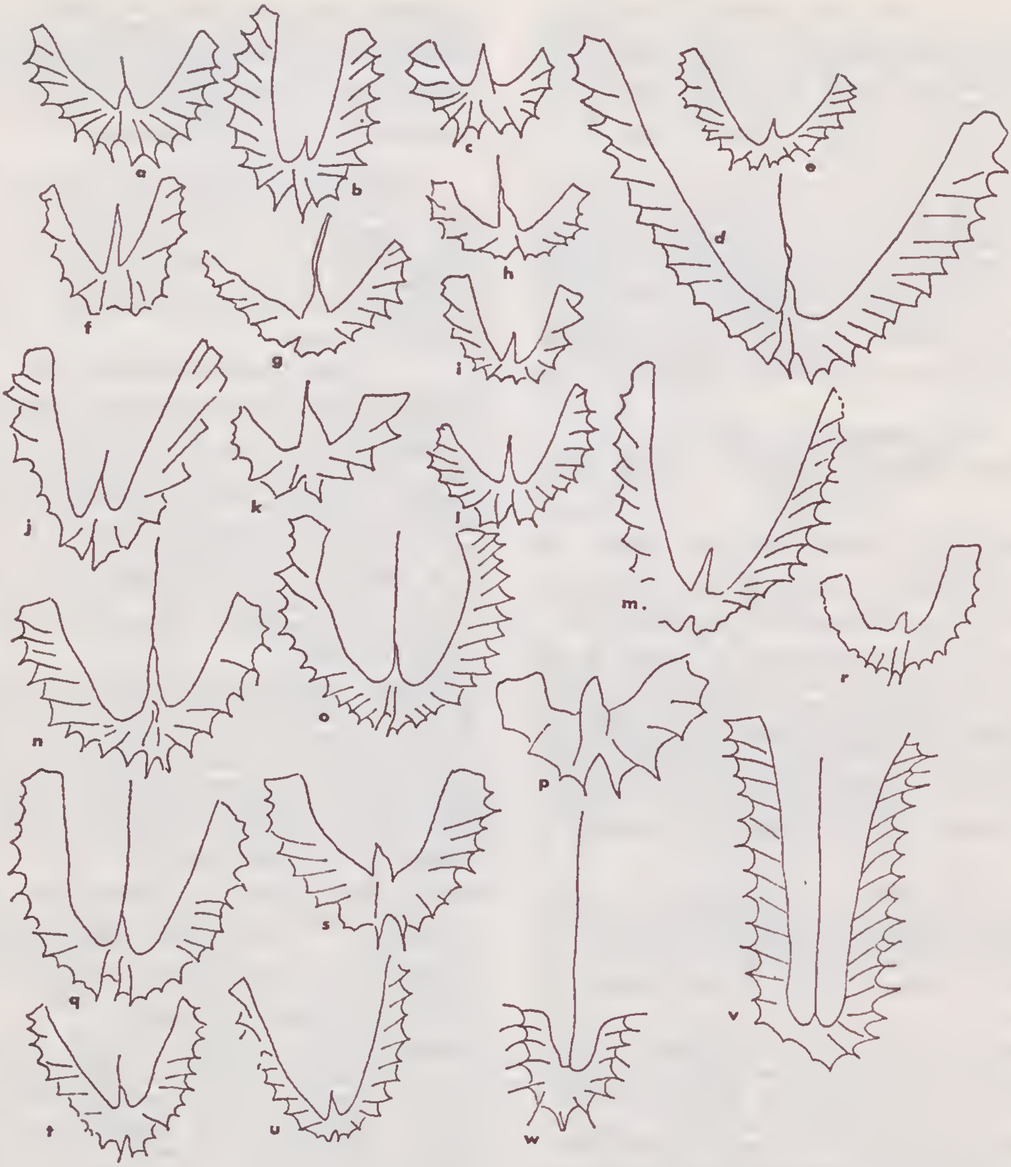


FIG. 5—*Isograptus victoriae* (a) SM A60286 Victoria Gully, Castlemaine, × 3, figured Skevington (1965). (b) SM A6319a Victoria Gully, Castlemaine, × 3. (c) SM A6319b Victoria Gully, Castlemaine, ×3. (d) SM A6320 Between Rifle Range and township, Castlemaine, × 3. (e) GS 4003 Durdidiwarrh Rd., Steiglitz, × 3. (f) GS 4004 Durdidiwarrh Rd., Steiglitz, × 6. (g) GS 4005 Old State School, Steiglitz, × 3. (h) GS 4006 Old State School, Steiglitz, × 3. (i) GS 4007 Mine dump, north of Steiglitz, × 3. (j) GS 4008 Durdidiwarrh Rd., Steiglitz, × 6. (k) GS 4009 Steiglitz, × 3. (l) GS 4010 Sutherlands Ck, Steiglitz, × 3. (m) GS 4011 *I. victoriae - I. maximus* transient, Yankee Gully, Steiglitz, × 3. (n) GS 4012 *I. victoriae - I. maximus* transient, Grahames Gully, Durdidiwarrh, × 3. (o) GS 4013 Durdidiwarrh Rd., Steiglitz, × 3. (p) GS 4014 Durdidiwarrh Rd., Steiglitz, × 3. (q) GS 4015 *I. victoriae - I. maximus* transient, Yankee Gully, Steiglitz, × 3. (r) GS 4016 *I. victoriae - I. maximus* transient, Yankee Gully, Steiglitz, × 3. (s) GS 4017 Brisbane Ranges, near Anakie North, ×3. (t) GS 4018 *I. victoriae - I. maximus* transient, Yankee Gully, Steiglitz, ×3. (u) GS 4019 Mariners Reef, Steiglitz, × 3. (v) (w) Salter's original figures, enlarged × 3 from *Quart. Jl. geol. Soc. London* 1853. '*Didymograptus caduceus*'.

Material: The figured specimens are SM No. A6319a, A6319b, A60286, Victoria Gully, Castlemaine, and SM No. A6320, between Military Rifle Range and Castlemaine. These are all catalogued as *Isograptus caduceus* var. *victoriae*. Specimens GS 400-4019, Steiglitz. Also figured are enlarged drawings of Salters' original figures (*Quart. Jl. Geol. Soc. London,* Vol. IX p. 87 Figure 1. 1853). In addition, approximately 250 examples were studied from GS, GV and NV collections. Specimen SM No. A 60286 is regarded as the typical example of the Victorian species.

Horizon and Localities: This is the zone fossil of the Castlemainian Ca2. It has a range from the base of this zone to the top of the Yapeenian zone Ya2. It occurs in the Castlemaine, Bendigo, Lancefield and Gisborne districts, in the Brisbane Ranges and the Mornington Peninsula.

Revised Diagnosis: Rhabdosome of two reclined stipes, dorsal walls slightly curved, diverging proximally at 250°, distally at 305° to 310°. Stipes about 1 cm long, but may be longer or shorter; 2·5 to 3·0 mm wide proximally, tapering to 2 mm or slightly less distally. Proximal thecae with gentle sigmoidal curvature, but th1^1 straight. Curvature decreases so that distal thecae are almost straight. Apertural margins concave, directed downwards in proximal thecae, outwards in others.

Description: The sicula is 4·5 to 5 mm long, and 1 mm wide at the aperture. A nema, sometimes quite long, is often attached. The sicula and th1^1 are in contact for almost the entire length, separation occurring in the apertural region so that there is a small ∩-shaped space between the apertural regions of the sicula and th1^1. The stipes are greatly curved giving a typical 'horse-shoe' shape to the rhabdosome. Gently tapering, the stipes have a width distally of 2 mm or slightly less, although rare specimens are as narrow as 1 mm.

The thecae are simple types: the proximal thecae are 2·0 mm long, 0·6 mm wide at the apertures; distal thecae are 1·2 to 1·5 mm long. Thecae number 11-12 in 10 mm; overlap is 0·9 or more.

Remarks: Harris regarded this form (his var. *victoriae*) as the '*forma typica*' of *Isograptus caduceus* in Victoria and it would appear that he regarded this, and *I. gibberulus* as conspecific. After a comparison of the Victorian *I. victoriae* and the European *I. gibberulus* (Table 7) the evidence points strongly to this being the case.

In *I. victoriae* the proximal thecae (except th1^1) are sigmoidally curved, with th1^1 and the distal thecae straight. Dorsal walls of the stipes are slightly curved. In *I. gibberulus* th1^1 and distal thecae are straight, the proximal thecae sigmoidally curved, or merely simply curved. Dorsal walls of the stipes are gently curved. In both, apertural margins are concave, directed downwards in the early thecae, and outwards in later thecae as the growth direction of the thecae changes from pendent to reclined. In both, denticles are prominent, directed downwards in the proximal thecae and outwards in the more distal. A study of Mobergs' and Elles' descriptions and figures show the same type and degree of variation in *I. gibberulus* as recorded by Harris for *I. victoriae.* The variation in the Victorian forms is illustrated by Fig. 5a, 5u.

Isograptus primulus Harris 1933

(Fig. 6a-d)

1933 *Isograptus caduceus* var. *primula* Harris
1971 *Isograptus victoriae primulus* Cooper

Material: Specimen GS No. 4021 figured here as Fig. 6b. Locality, mine dump near site of former

Table 7

	Stipe length Cm	Proximal width of stipe mm.	Distal width of stipe mm	Thecae in 10 mm	Divergence angle proximally	Divergence angle distally	Thecal overlap	Length of proximal thecae mm.	Length of distal thecae mm.	Width of proximal thecae mm.	Width of distal thecae mm	Apertural margins	Direction of denticle
I. victoriae	1+	2.5-3.0	2-	11-12	250°	305°-310°	0.9	2.0	1.2-1.5	0.6	0.5	Conc.	Out
I. gibberulus	1-2	2.5.	1+	13	260°	310°	0.9	2.0	1.3	0.7	0.5	Conc.	Out

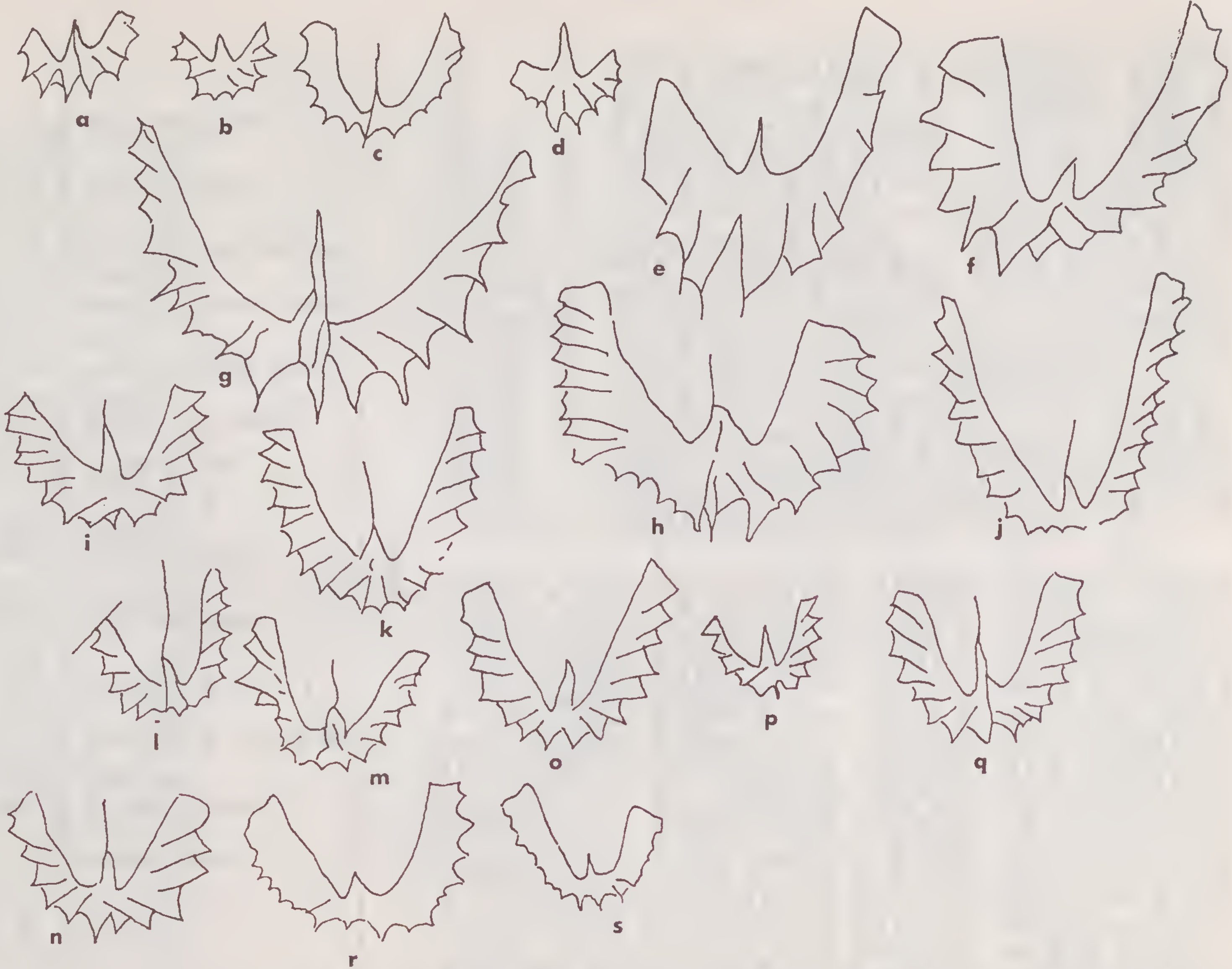


FIG. 6—*Isograptus primulus* (a) GS 4021 Birmingham Mine, Steiglitz, × 5. (b) GS 4020 Steiglitz township, ×5. (c) GS 4022/ GV 7712 Steiglitz township, × 5. (d) GS 4023 Mariners Gully, Steiglitz, × 5. *Isograptus lunatus* (e) GV 6923 Sutherlands Ck, Steiglitz, × 5. (f) SM A6318 East of Victoria Gully, Castlemaine, × 5. (g) GS 4024 Slate Quarry, Moorabool Rd., Meredith, × 5. (h) GS 4025 Steiglitz, × 10. (i) GS 4026 Durdidiwarrh, × 5. (j) GS 4027 Durdidiwarrh, × 5. (k) GS 4028 Durdidiwarrh, × 5. (l) GS 4029 Durdidiwarrh, × 5. (m) GS 4030 Durdidiwarrh, × 5. (n) GS 4031 Durdidiwarrh, × 5. (o) GS 4032 Durdidiwarrh, × 5. (p) GS 4033 Durdidiwarrh, × 5. (q) GS 4034 Durdidiwarrh, × 5. (r) GS 4035 Durdidiwarrh Rd, Steiglitz, × 5. (s) GS 4036 Durdidiwarrh Rd, Steiglitz, × 5.

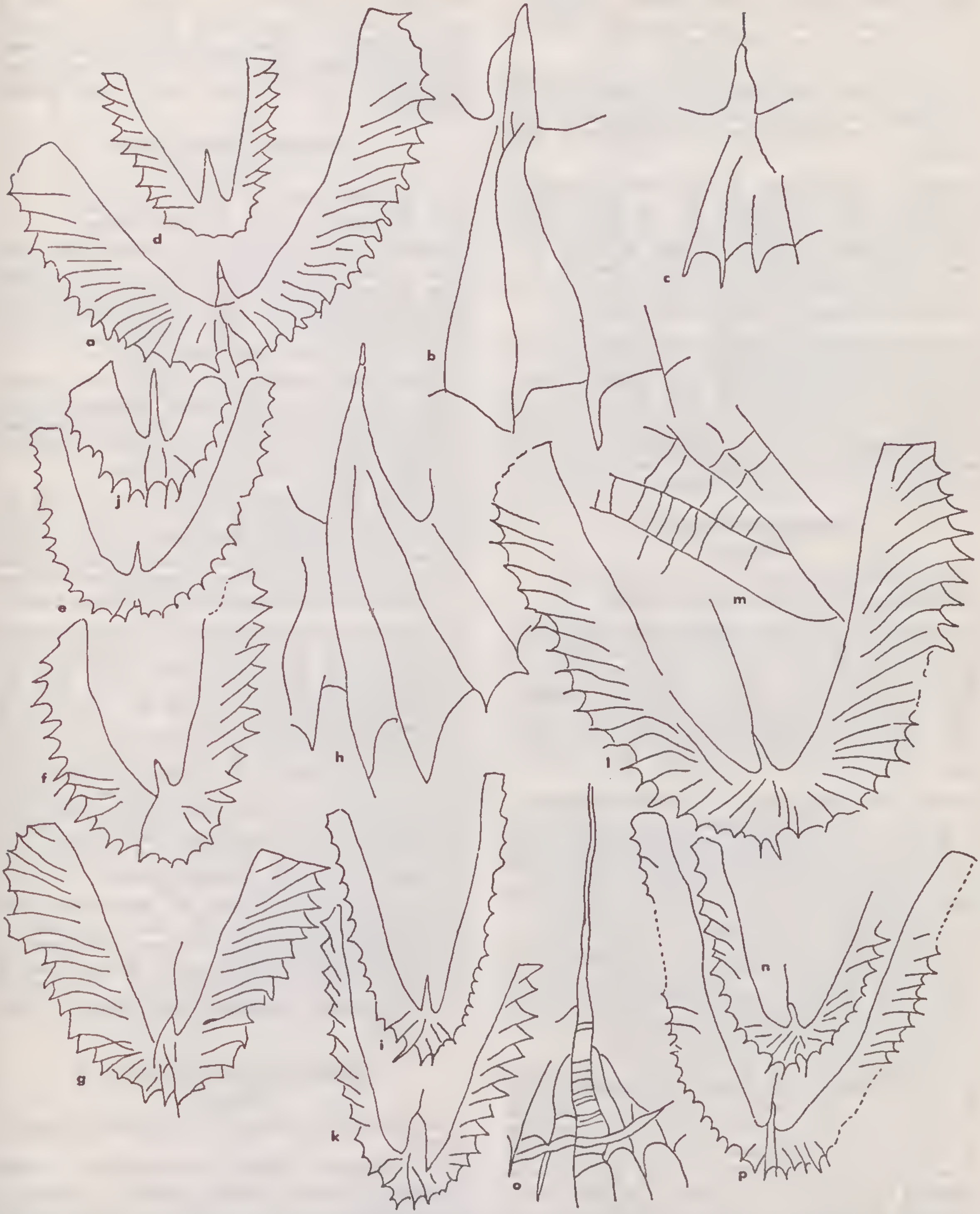


FIG. 7—*Isograptus maximus* (a) SM A6321c Bullengarook Slate Quarry, Gisborne, ×3. (b) SM A6321a showing proximal region. Same locality as (a), × 25. (c) SM A6321d showing proximal region. Same locality as (a), × 12·5. (d) GS 4037 Moorabool River, Meredith, ×3. (e) GS 4038 Sutherlands Ck, Steiglitz, × 3. (f) GS 4040 Anakie Gorge, × 3. (g) GS 4041 Moorabool River Bridge, Steiglitz-Meredith Rd, × 3. (h) GS 4041 detail of proximal region, × 12·5. (i) GS 4042 Steiglitz, × 3. (j) GS 4043 Steiglitz, × 3. (k) GS 4044 Yankee Gully, Durdidiwarrh, × 3. (l) GS 4045 Grahames Gully, Steiglitz, × 3. (m) GS 4045 detail of thecae, × 12·5. (n) GS 4046 Yankee Gully, Steiglitz, × 3. (o) GS 4047 Little River Gorge, Brisbane Ranges, × 3. (p) GS 4048, Steiglitz, × 3.

Steiglitz State School, Steiglitz, Victoria. Other material examined included 3 specimens from Steiglitz. All are preserved as white films on grey slate.

Horizon and Localities: Found as an important member of Chewtonian Ch2 and Castlemainian Ca1 assemblages: rare in Ca2 beds. Recorded from Castlemaine, Chewton, Bendigo, Brisbane Ranges and Steiglitz.

Diagnosis: Rhabdosome of two stipes diverging initially at 180°, but distally 290° to 300°. Stipes taper rapidly so that distally they are about ⅓ the width proximally. Apertural margins of thecae concave directed downwards in proximal thecae, outwards in distal thecae. Denticles small, directed downwards. Development isograptid (*gibberulus*) type.

Description: The sicula is long and narrow, 2·5 to 3 mm in length, apertural width 1 mm. The stipes are short, each stipe consisting of only about 4 thecae. Proximally the stipes are 2 mm wide, narrowing distally to 0·7 mm. The thecae are straight, simple tubes: proximal thecae are 1 mm long and 0·5 mm wide; distal thecae are 0·4 to 0·5 mm long. Thecal spacing is 10 to 12 in 10 mm, overlap 0·8 to 0·9.

Isograptus lunatus Harris

(Fig. 6e-s)

1933 *Isograptus caduceus* var. *lunatus* Harris
1971 *Isograptus victoriae lunatus* Cooper

Material: GV No. 6293, Sutherlands Creek. Steiglitz. Figured by Harris (1933) as Text figure 5, figured this paper as Fig. 6e. SM No. A 6318 is shown as Fig. 6f, east of Victoria Gully, Castlemaine. Other material examined: 11 specimens from Castlemaine, and 17 from Steiglitz. Of these GS 4024-4036 are figured. Preserved as thin films on grey slate.

Horizon and Localities: This species is the zone fossil for the Castlemainian Zone Ca1. It first appears at the top of the Chewtonian Ch2 and persists, with diminished importance to the Yapeenian Ya1. It has been recorded from Bendigo, Castlemaine, Chewton, Steiglitz, Brisbane Ranges and Mornington Peninsula.

Diagnosis: Two uniserial reclined stipes of uniform width, with straight or uniformly curved dorsal walls, angle of divergence 295° to 310°. Thecae straight, simple tubes, apertural margins concave and directed upwards or outwards, but downwards on initial thecae. Development isograptid (*gibberulus*) type.

Description: The sicula is 1 mm long and 0·8 mm wide at the aperture. The stipes have a uniform width of 1·0 to 1·5 mm, length rarely exceeds 1 cm. The thecae are straight, 1·0 mm long and 0·6 mm wide at the aperture. Denticles are small but prominent. Thecal spacing varies from 14 in 10 mm in some examples to 11 in 10 mm in others. Overlap is more than 0·9. Distally, the thecal inclination becomes sharper; the fifth theca of each stipe is inclined at 95° to 100° to the stipe axis; the most distal thecae are inclined at less than 40°. In spite of this change, stipe width is uniform.

Remarks: This species has a rhabdosome which is more robust and larger than that of *I. primulus*, while the angle of divergence is significantly greater. Later forms (from Ca2 to Ya1) tend to have larger rhabdosomes, but otherwise there is no marked difference.

Isograptus maximus Harris

(Fig. 7a-s)

1933 *Isograptus caduceus* var. *maxima* Harris
1971 *Isograptus victoriae maximus* Cooper

Material: SM No. A6321e Bullengarook Slate Quarry, near Gisborne, Victoria, Fig. 7a, 3 specimens from Gisborne, SM collection; 16 from Steiglitz and 5 from Castlemaine, GV and GS collections. Preserved as white films on grey slate. Figured are SM No. A 6321a, d, GS 4037, 4038, 4040-4047.

Horizon and Localities: Zonal fossil for the Castlemainian Ca3, the form is equally prominent in Ca3 and Ya1 beds. It ranges up into the Darrwilian Da1. Recorded from Bendigo, Castlemaine, Gisborne, Macedon, Steiglitz, and Brisbane Ranges.

Diagnosis: Rhabdosome two reclined stipes of uniform width with angle of divergence 300° to 310°. Stipes straight or with dorsal walls slightly curved. Thecae pendent in proximal region, distally reclined to scandent, curved; apertures concave, directed downwards in proximal thecae, outwards in distal thecae.

Description: The sicula may be 2·0 to 3·5 mm long and 1 mm wide, sometimes with a prominent nema. Two types are known: the large form (e.g. No. A 6321c) and the small form (e.g. SM No. A 6321b). In both the stipe width is about the same (1·5 to 2·00 mm) but in the large form, rarely less than 2·0 mm. The width of the stipe is constant throughout the rhabdosome. In the larger form, thecae are 4 mm long and 0·8 mm wide; in the smaller form, 2·5 mm long and 0·7 mm wide. In both forms, thecae number 11 to 12 in 10 mm with overlap 0·9 or more. The thecae are gently curved: curvature may be concave downwards or gently sigmoidal.

Remarks: Of the two forms, the larger is the more common; both are quite distinct from *I. victoriae*. In particular, the stipes have a uniform width, and the thecae show distinct differences. It is quite clear in some examples (e.g. SM No. 6321a and A6321d) that the proximal development is isograptid (*gibberulus*) type.

Isograptus maximodivergens Harris

(Fig. 8a-i)

1933 *Isograptus caduceus* var. *maximo-divergens* Harris
1971 *Isograptus victoriae maximo-divergens* Cooper

Material: Specimen SM No. A6322a, Rifle Range, Castlemaine, figured here as Fig. 8a. Also figured are A 6322b from the same locality, and A 22750, Loc. Ba71 Gisborne. Other material examined: 21 specimens GS collection from Gisborne, Steiglitz and Castlemaine. Figured GS 4049-4053 from Steiglitz.

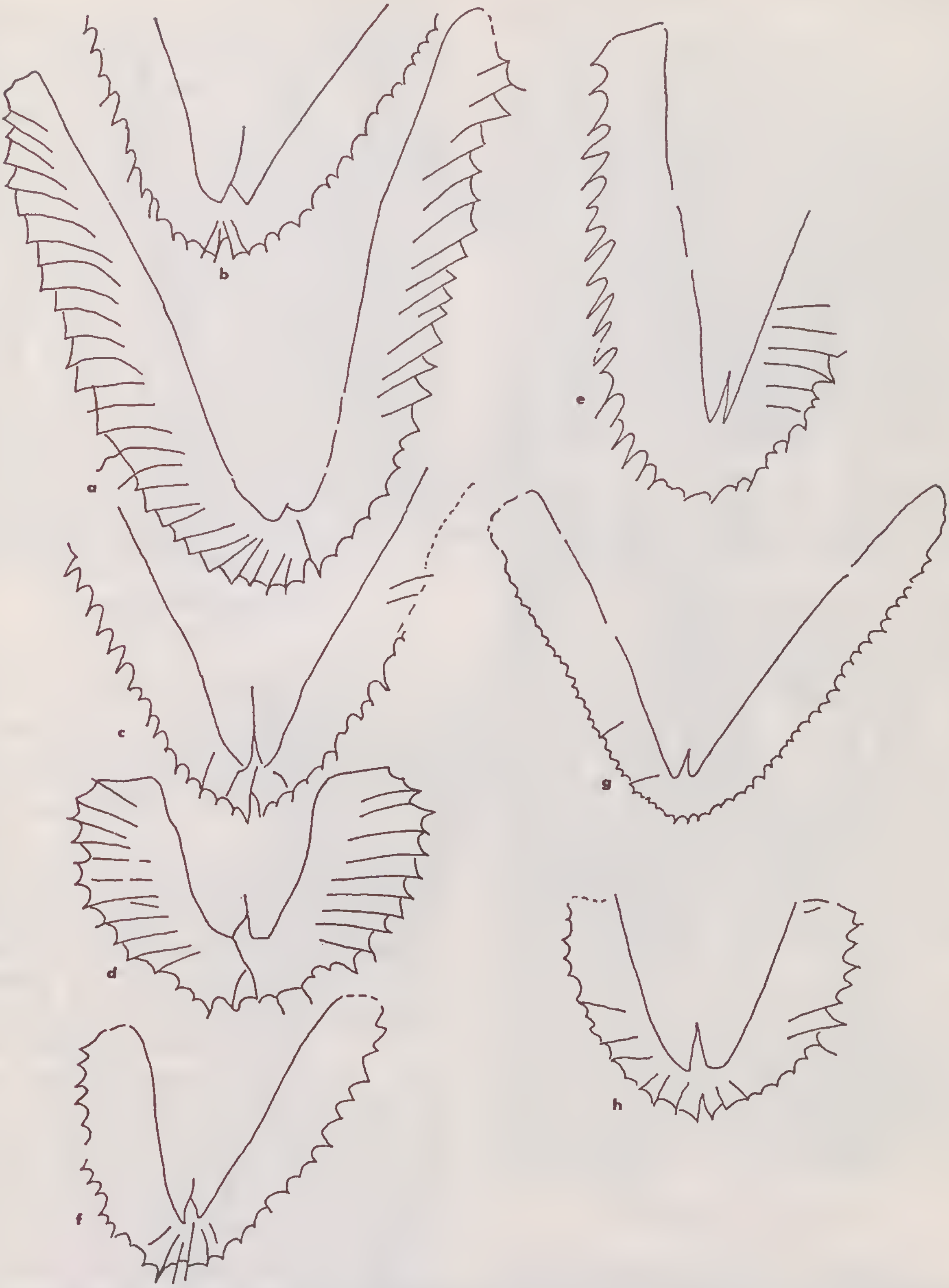


FIG. 8—*Isograptus maximodivergens* (a) SM A6322a Rifle Range, Castlemaine, × 3. (b) SM A6322b Rifle Range, Castlemaine, × 3. (c) SM A22750 Loc. Ba71, Gisborne, × 3. (d) GS 4049 Steiglitz, × 3. (e) GS 4050 Moorabool River, Sheoaks, × 3. (f) GS 4051 Moorabool River Bridge, Steiglitz-Meredith Rd, × 3. (g) GS 4052 Slate Quarry, Darragh, Meredith, × 1·8 approx. (h) GS 4053 Same locality as (g), × 3.

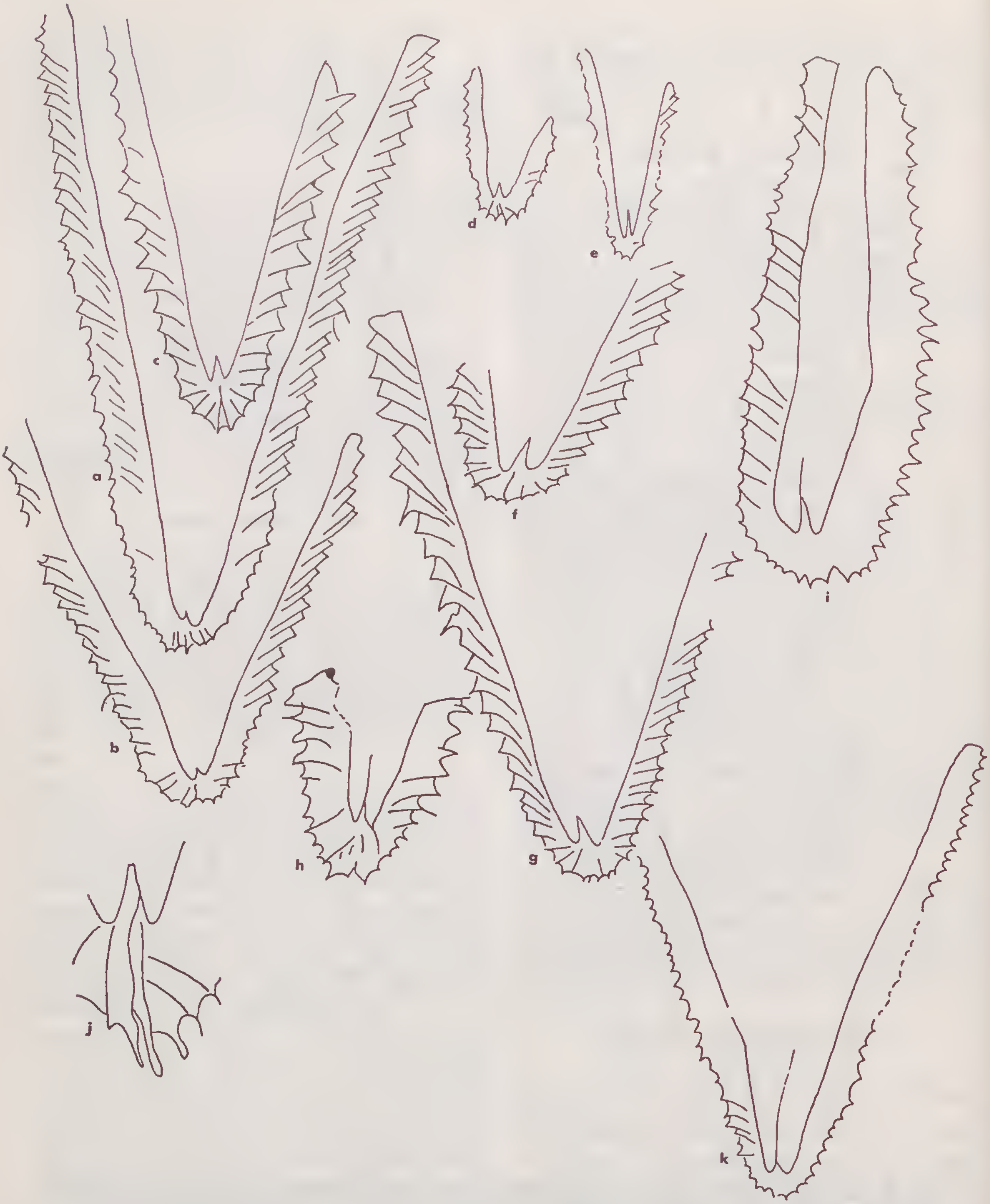


FIG. 9—*Isograptus divergens* (a) SM A6323a Chinamans Ck, Muckleford, × 2. (b) SM A6323b Same locality as (a), × 2. (c) GS 4054 Little River, Brisbane Ranges, × 3. (d) GS 4055 Small form, Sutherlands Ck, Steiglitz, × 3. ? *Isograptus divergens* (e) GS 4056 Similar to example figured by Harris (1933) as 'degenerate form'. Collected high Ca2 beds, Yankee Gully, Steiglitz, × 3. *Isograptus divergens* (f) GS 4057 Cutting in Steiglitz-Maude Rd, south of Hanover Fault, × 3 (Darrwilian). (g) GS 4058 Same locality as (f), ×3. (h) GS 4059 Coolebarghurk Ck, Meredith, × 3. (i) GS 4060 Brisbane Ranges, near Anakie Gorge, × 3. (j) GS 4061 Same locality as (i), × 6. (k) GS 4062 Moorabool River, Sheoaks, × 1·8 approx.

Horizon and Localities: A typical Yapeenian form, this species first appears at the base of Ya1 and persists to the top of Darrwilian Da2. Recorded from Bendigo, Castlemaine, Macedon and Gisborne districts, the Brisbane Ranges and Steiglitz.

Diagnosis: Two stipes reclined, angle of divergence 315° to 325°. Dorsal stipe walls straight or slightly curved. Stipes narrow in proximal region, widening at about the third theca in each stipe and then maintaining constant width. Thecae long, slightly curved.

Description: The sicula is 3 mm long, and 0·6 to 0.75 mm apertural width. A nema is usually present. Stipes are 2·5 to 3 cm long, 2·5 mm wide proximally widening to about 4 mm at about the third theca on each stipe. Some examples show a narrowing in the extreme distal region, but normally after widening, width is constant. Thecae are 4 mm long and 1 mm wide, but the first 2 or 3 thecae on each stipe are shorter. Thecae are simple, straight or with gentle curvature, concave downwards. Denticles are prominent and are directed downwards on the curved thecae, outwards on the straight. Thecae number 8 to 9 in 10 mm, and overlap is almost complete.

Some forms are known with stipes much longer than the figured examples: some are known with stipes 5 cm long and 5 mm wide.

Isograptus divergens Harris

(Fig. 9a-k)

1933 *Isograptus caduceus* var. *divergens* Harris
1971 *Isograptus victoriae divergens* Cooper

Material: SM No. A6323a and A6323b, Chinamans Creek, Muckleford. These examples are preserved as limonite films on fawn slate. Other material examined: 7 specimens as white films on black slate, GS collection, Steiglitz. Of these GS 4050-4062 are figured.

Horizon and Localities: This form is present in Yapeenian Ya1 and Ya2 assemblages. It persists in diminishing importance to the top of Darrwilian Da3. Recorded from Bendigo, Castlemaine, Gisborne and Macedon districts, Steiglitz, and Brisbane Ranges.

Diagnosis: Two stipes diverging at 330° to 335°. Stipes show slight distal tapering; dorsal walls straight or slightly curved. Thecae curved or straight, number 10 to 11 in 10 mm, overlap 0·8 to 0·9.

Description: The sicula is relatively small: 2·5 to 3 mm long with an apertural width of 1 mm. The stipes are up to 6 cm long and 2·0 to 2·5 mm wide. The dorsal stipe walls may be straight, but more commonly they have a gentle irregular curvature. The thecae are 3·0 to 3·5 mm long and 0·9 mm wide, although they may be narrower. They are simple tubes, straight, or with a slight downwardly concave curvature. The apertural margins are straight and make an angle of 90° or more with the ventral thecal wall.

Remarks: The stipes in this species are relatively narrower than those of *I. maximodivergens.* Harris described the rhabdosome as being 'less robust' than that of *I. divergens.* The dimensions given above are typical, but both larger and smaller examples have been recorded.

Isograptus imitatus Harris

(Fig. 10a-c)

1933 *Isograptus caduceus* var. *imitata* Harris

Material: SM No. A60288, Fitzgeralds Quarry, Gisborne, figured Skevington (1968) and figured here as Fig. 10a. Also figured are A60287 from the same locality, also figured by Skevington (1968) and figured here as Fig. 10b. Also figured are A60287 from the same locality, also figured by Skevington (1968) and A 60234 Bullengarook Slate Quarry, Gisborne. All are preserved as white films on black slate. In addition to the figured material, three specimens from Muckleford, Victoria, were examined.

Horizon and Localities: This species first appears near the top of the Castlemanian Ca3 and persists into the basal beds of the Darrwilian Da1. Recorded from Gisborne and Castlemaine (Muckleford) districts.

Diagnosis: Two reclined stipes, near scandent, diverging at 325° to 330°. Sicula very long and narrow. Thecae curved, more so proximally than distally. Proximal thecae pendent and almost straight, distal thecae reclined.

Description: In the few specimens examined there appears to be considerable variation, but some features are relatively constant. The sicula is long, 8 mm or more, and narrow, with an apertural width of 1 mm. There is frequently a long nema. The stipes vary in length, maximum 1·5 cm. They are widest in the proximal region (3 to 3·5 mm) narrowing to 2-2·2 mm distally. Thecae are 1·5 mm long and 0·5 mm wide, number 8 to 10 in 10 mm and overlap 0·95 to 1·0. The first two thecae of each stipe have apertures opening downwards; the intermediate thecae open outwards, and the distal thecae upwards. The denticles are very prominent and are directed downwards or outwards. It is characteristic of this species, as for *I. victoriae* that $th1^1$ and the sicula, in contact for almost their entire length, separate apertually, so that there is between the apertures of the two, a ∩-shaped space.

Remarks: Harris regarded this species as a catagenetic variety of *I. caduceus* and considered that it resembled the much earlier *I. lunatus.* However, it has a much more robust rhabdosome and the morphology of the proximal region is quite distinct. Harris erred in stating the *I. imitatus* persists into the Upper Ordovician. There is no record, so far as can be ascertained, of it in beds higher than the lowest Darriwilian.

Isograptus velatus Harris

(Fig. 10d, e)

1933 *Isograptus caduceus* var. *velata* Harris

Material: GV No. 31331. Locality L34, Lancefield, figured here as Fig. 10d. Also figured is SM No. A6323d Muckleford, which may be a juvenile form of this species, or may be a juvenile *Pseudisograptus.*

HORIZON AND LOCALITIES: A very rare Yapeenian form, known with certainty only from Lancefield.

DIAGNOSIS: Two tapering stipes diverging at 330°-340°, dorsal walls gently curved. Thecae straight to slightly curved, apertural margins straight to slightly concave, directed outwards even in the proximal thecae. Proximal development modified isograptid (*gibberulus*) type.

DESCRIPTION: The sicula is 2·5 mm long. The stipes taper from a width of about 2 mm proximally to 1·0 mm distally. The stipes are 5 mm long. Proximal thecae are 1·5 mm long, distal thecae 0·9 mm, width of thecae is 0·6 to 0·7 mm. Thecae number 9 to 10 in 10 mm, overlap 0·6.

REMARKS: Certain features of this species suggest that it has affinities with *Pseudisograptus*: notably the outward direction of apertures of th1^1 and th1^2. However, with only one certain specimen of this form, reference to the genus *Pseudisograptus* could not be justified at this stage.

Isograptus tenuis Harris

(Fig. 10f)

1933 *Isograptus caduceus* var. *tenuis* Harris

MATERIAL: Two specimens GS 4063, 4064 preserved in white on pale slate.

HORIZON AND LOCALITIES: A rare form known only from Locality Ba67, Gisborne. Upper Ordovician, it does not have the range Castlemainian to Upper Ordovician given by Harris.

DIAGNOSIS: Small rhabdosome with slender stipes diverging at 300°. Thecae simple straight tubes, apertural margins straight. Denticles weak.

DESCRIPTION: The stipes are 6 mm long, and 0·6 mm wide. The sicula, 1 mm long, is not prominent. The thecae are simple straight tubes, 0·7 mm long and 0·4 mm wide, number 12 to 14 in 10 mm, overlap 0·4. Apertural margins are directed outwards.

Isograptus ovatus (T. S. Hall)

(Fig. 11a, b)

1902 *Didymograptus ovatus* T. S. Hall
1933 *Isograptus ovatus* Harris

MATERIAL: A single complete specimen, the lectotype, SM No. A 6345, 'The 8 Mile', Howqua River. Preserved as a fine film on black slate, and one incomplete specimen from Moorabool River, Steiglitz (GS 4039).

HORIZON AND LOCALITIES: A very rare form found from the base of the Yapeenian Ya1 to the base of Ya2. Known from 6 examples only: Tabberabbera (1) Turners Quarry, Bittern (2), 'The 8 Mile', Howqua (2), Steiglitz (1).

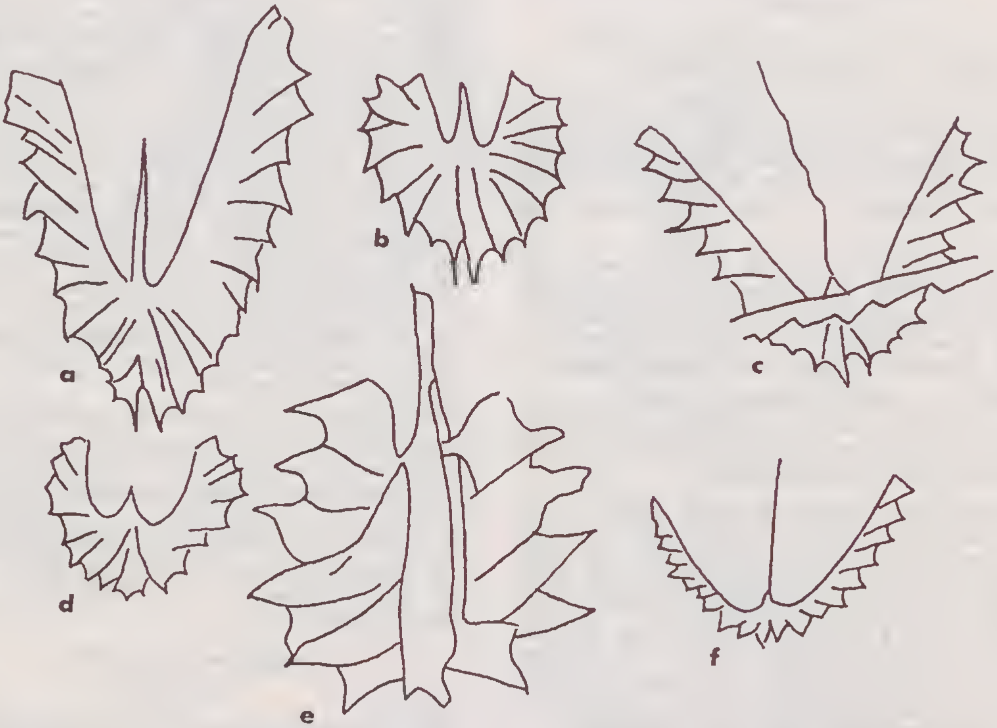


FIG. 10—*Isograptus imitatus* (a) SM A80288 Fitzgeralds Quarry, Gisborne, figured Skevington (1968), × 4. (b) SM A60287 Same locality as (a), figured Skevington (1968), × 4. (c) SM A60234, Bullengarook Slate Quarry, Gisborne, × 4. *Isograptus velatus* (d) GV 31331 Lectotype, Lancefield, × 4. ? *Isograptus velatus* (e) Juvenile form SM A6323d Chinamans Ck, Muckleford, × 8. *Isograptus tenuis* (f) GS 4063 Lectotype. Loc. Ba67, Gisborne, × 4.

REVISED DIAGNOSIS: Two scandent stipes, uniform in width, with curved dorsal margins, converging distally. Thecae curved, with strongly concave apertural margins.

DESCRIPTION: The sicula is 3·5 mm long and is narrow. The stipes are 1 cm long, with uniform width of 1·8 mm. Thecae are curved, 1·5 mm long, 0·5 mm wide. Thecal spacing is 12 in 10 mm with overlap 0·5 or slightly more.

REMARKS: This rare form is noted for the distinctive ovate outline of the rhabdosome. The rather thick sicular region is the only basis for regarding it as related to *Pseudisograptus*: at present there is inadequate data to warrant reference of the form to this genus.

Isograptus forcipiformis Ruedemann

(Fig. 11a-i)

1904 *Isograptus forcipiformis* Ruedemann (1904)
1933 *Iosgraptus forcipiformis* Harris (1933)
1968 *Isograptus forcipiformis* Skevington (1968)

MATERIAL: Fourteen examples from Strathfieldsaye, near Bendigo preserved as purple films on fawn slate; three from Steiglitz preserved as carbonaceous films on brown shale.

HORIZON AND LOCALITIES: Base of Yapeenian Ya1 to the top of Darriwilian Da3. It is most common in this upper zone. It has been recorded from the Bendigo, Gisborne and Steiglitz districts.

DESCRIPTION: The rhabdosome consists of two scandent stipes with dorsal margins straight and parallel. The stipes are 0·7 to 1·5 cm long and 1·0 to 1·2 mm wide. In the proximal region the stipes may be up to 4 mm wide. Distance between the dorsal walls of the two stipes is 0·8 to 1·2 mm. The sicula is up to 5 mm long and is narrow. Thecae are about 1 mm long, apparently 0·4 mm to 0·5 mm wide, but possibly wider (see 'Remarks'). Thecae are curved, but the curvature decreases in the distal thecae. Apertures generally concave, directed outwards, or in some examples, those of the distal thecae may be directed upwards. Denticles pronounced, directed downwards. Thecae number 9-11 in 10 mm, overlap almost complete.

REMARKS: Ruedemann regarded this species as an extreme development of *I. caduceus* in its divergence and the slenderness of the stipes. Harris regarded it as the final stage before concrescence to produce *Skiagraptus*. This view is now untenable on both palaeontological and stratigraphic evidence, although in one example (e.g. Fig. 11d) there are some

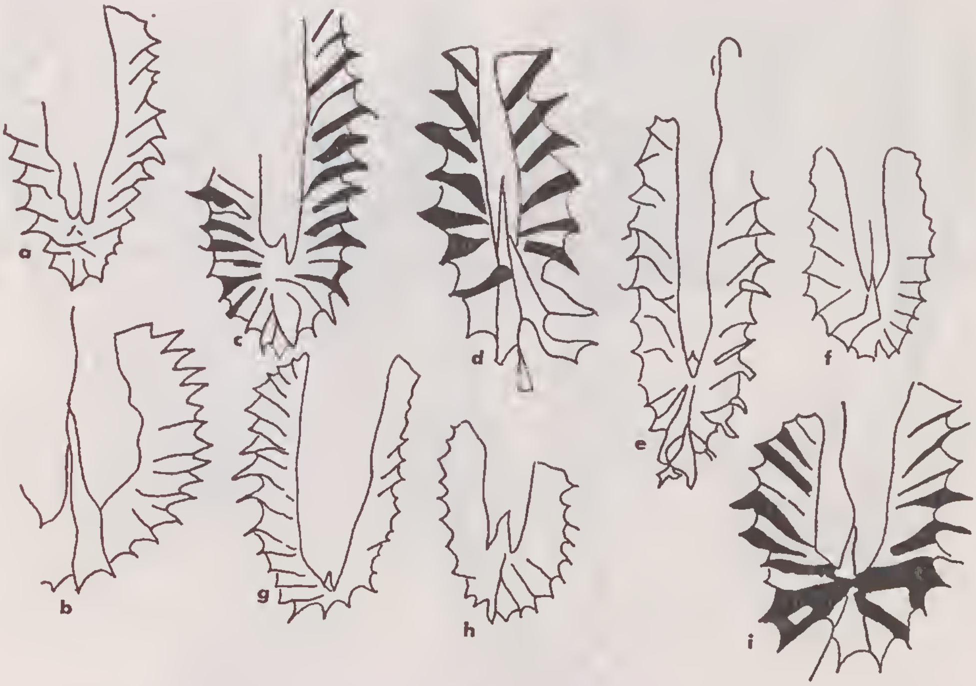


FIG. 11—*Isograptus ovatus* (a) SM 6345 'The 8 Mile', Howqua, × 3. (b) GS 4039 Moorabool River Bridge, Steiglitz-Meredith Rd, ×3. *Isograptus forcipiformis* (c) SM A6341 Strathfieldsaye, × 3. (d) SM A60291 Jacksons Ck, Gisborne, × 6. (e) SM A60290a Strathfieldsaye, × 3. (f) GS 4065 Steiglitz-Maude Rd, × 3. (g) GS 4066 Same locality as (f), × 3. (h) GS 4067 Moorabool River, Sheoaks, × 3. (i) GS 4068 Road cutting south of Hanover Fault, Steiglitz-Maude Rd, × 3.

skiagraptid aspects in the proximal region, particularly in the outward direction of growth of th1¹. However, the proximal development is clearly isograptid, though of a modified type. Lacking any definite evidence to justify reference to another genus, this form is here retained in the genus *Isograptus*.

One interesting feature of this species is the incipient monopleural arrangement of the thecae, with a distinct lateral overlap shown in the highly compressed specimens as a very dark and slightly thicker band of limonite. With this arrangement, in vertical plan the rhabdosome would have a broad, open shape.

Isograptus pertensus Harris

(Fig. 12a-f)

1933 *Isograptus caduceus* var. *pertensa* n. var. Harris
1968 *Isograptus pertensa* Beavis and Beavis

MATERIAL: Lectotype GV No. 6719 Sutherlands Creek, Steiglitz. Preserved as white film on black, strongly cleaved slate. Seven other specimens from the same locality and four from the Moorabool R. Sheoaks, downstream of Coolebarghurk Creek Junction.

HORIZON AND LOCALITIES: Range from transitional Ca3-Ya1 beds to Darriwilian Da1. Known only from Steiglitz and a small form from Lancefield.

DIAGNOSIS: Two long, slender, scandent stipes diverging at 340°. Stipes straight to gently curved, tapering distally. Thecae small, simple; apertural margins concave, denticles small.

DESCRIPTION: Rhabdosome large, with stipes up to 10 cm long; proximally 3 mm wide, distally 1·5 mm. The sicula is small: 8 mm long and less than 1 mm wide at the aperture. Proximal thecae 7 to 8 in 10 mm, 4 mm long, 0·8 mm wide, strongly denticulate. Distal thecae 6 to 7 in 10 mm, smaller, less denticulate. Overlap almost complete.

REMARKS: A small form, identical in all respects except size, has been recorded from the Lancefield district. Harris referred to this as *I. caduceus* var. *horrida* but there seems no justification for regarding

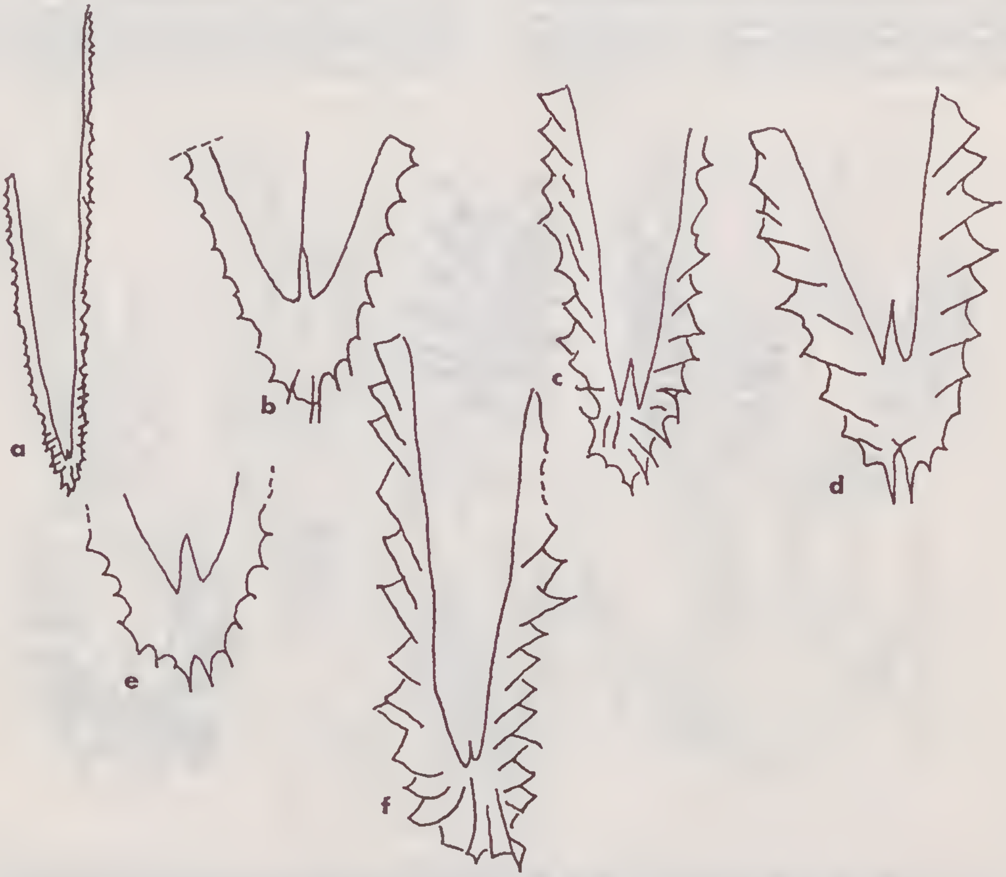


FIG. 12—*Isograptus pertensus* (a) GV 6719 Lectotype. Sutherlands Ck, Steiglitz, × 0·7 approx. (b) GS 4069 Coolebarghurk Ck, Meredith, × 4 approx. (c) GS 4070 Moorabool River, Sheoaks, × 4 approx. (d) GS 4071 Same locality as (c), × 4 approx. (e) GS 4072 Anakie Gorge, × 4 approx. (f) GS 4073 Collected from type locality at point where Hanover Fault is crossed by Sutherlands Ck, near Mariners Gully, × 4 approx.

it as a separate form. *I. pertensus* is notable for the relatively primitive thecae, reminiscent of some of the lower Castlemainian forms; Harris regarded it as a catagenic variety of *I. caduceus.*

Isograptus harrisi n. sp.

(Fig. 13a,e)

MATERIAL: Holotype GS 4075. Maude Road, Steiglitz. Fifteen other specimens from the same locality of which four are figured.

DERIVATION OF NAME: Named for the late Dr. W. J. Harris.

HORIZON AND LOCALITIES: Darriwilian, Da1. Known from Maude Road, Steiglitz, where beds are exposed in a road cutting about 1·5 km south of Steiglitz cemetery. Also collected on Coolebarghurk Creek near Meredith.

DIAGNOSIS: Small *Isograptus* with long prominent sicula. Stipes taper slightly. Thecae simple, with high overlap. Proximal development isograptid (*gibberulus*) type.

DESCRIPTION: The sicula is relatively long (3·6 mm including ventral process) and narrow, 0·7 mm at aperture. Th1^1 arises high up on the sicula and grows down along. and apparently in contact with, the sicula for its entire length. Th2^1 appears to rise high up on th1^1 at first and then curve outwards. Thecae are simple, overlap 0·85 to 1·0, dorsal walls slightly curved, apertural margins concave, sometimes with a fine denticle. Apertures of proximal thecae directed downwards or slightly outwards; all other thecae have apertures directed outwards. Thecae number 13-15 in 10 mm. Initially the stipes are 1·8 mm to 2·0 mm wide, but taper rapidly to 0·8 to 0·9 mm. Dorsal walls are curved. Initially the angle of divergence is 180°; distally it may be as high as 330°. The rhabdosome is small, usually 4 mm or less wide.

REMARKS: This small form occurs relatively abundantly at the type locality but is rare at the other locality from which it was recorded. Both localities are high Da1 transitional to Da2, with *Glyptograptus austrodentatus, G. intersitus, Paraglossograptus etheridgei* and *Tristichograptus ensiformis* as associates.

The proximal development is almost certainly of the isograptid (*gibberulus*) type, although some curvature of the distal parts of the proximal thecae is a modification of this type. The form is morphologically quite distinctive from other Darriwilian isograptids.

Sub-family CARDIOGRAPTINAE Mu and Zhan 1966

Genus **Oncograptus** T. S. Hall 1914

Oncograptus upsilon T. S. Hall

(Fig. 14a-i)

1914 *Oncograptus upsilon* T. S. Hall

MATERIAL: Three specimens of the subspecies *O. upsilon biangulatus* preserved in relief from the El Paso Limestone, Texas. Twenty-two compressed specimens from Victoria: brown or white films on dark slate.

HORIZON AND LOCALITIES: Zonal fossil for the Yapeenian Ya1. The species ranges up into Ya2. The subspecies *O. upsilon biangulatus* Harris and Keble is an upper Ya1-lower Ya2 form. Occurs at Bendigo, Castlemaine, Gisborne, Macedon, Mornington Peninsula, Brisbane Ranges, Steiglitz. In the Brisbane Ranges it has been recorded from Da1 beds.

DESCRIPTION: Rhabdosome initially biserial, distally consisting of two uniserial stipes. The biserial part of the rhabdosome is 1·5 to 2 cm long, and with a maximum width of 1·3 cm at the bifurcation. It is 4 to 5 mm wide proximally. The uniserial stipes are of uniform width, up to 5 mm and may be 2 cm long. Thecae in the biserial part of the rhabdosome are 5 mm long and 1 mm wide and are sigmoidally curved

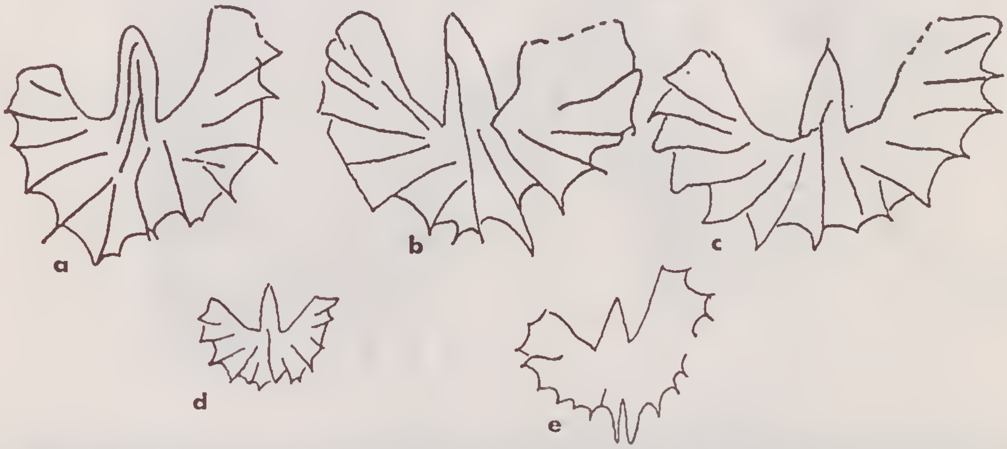


FIG. 13—*Isograptus harrisi* (a) GS 4075 Holotype. New road cutting on Steiglitz-Maude Rd, 1·5 km south from new Steiglitz cemetery, × 9. (b) GS 4074 Same locality as (a), × 9. (c) GS 4076 Same locality as (a), × 9. (d) GS 4077 Same locality as (a), × 4·5. (e) GS 4078 Coolebarghurk Ck, Meredith, × 4·5.

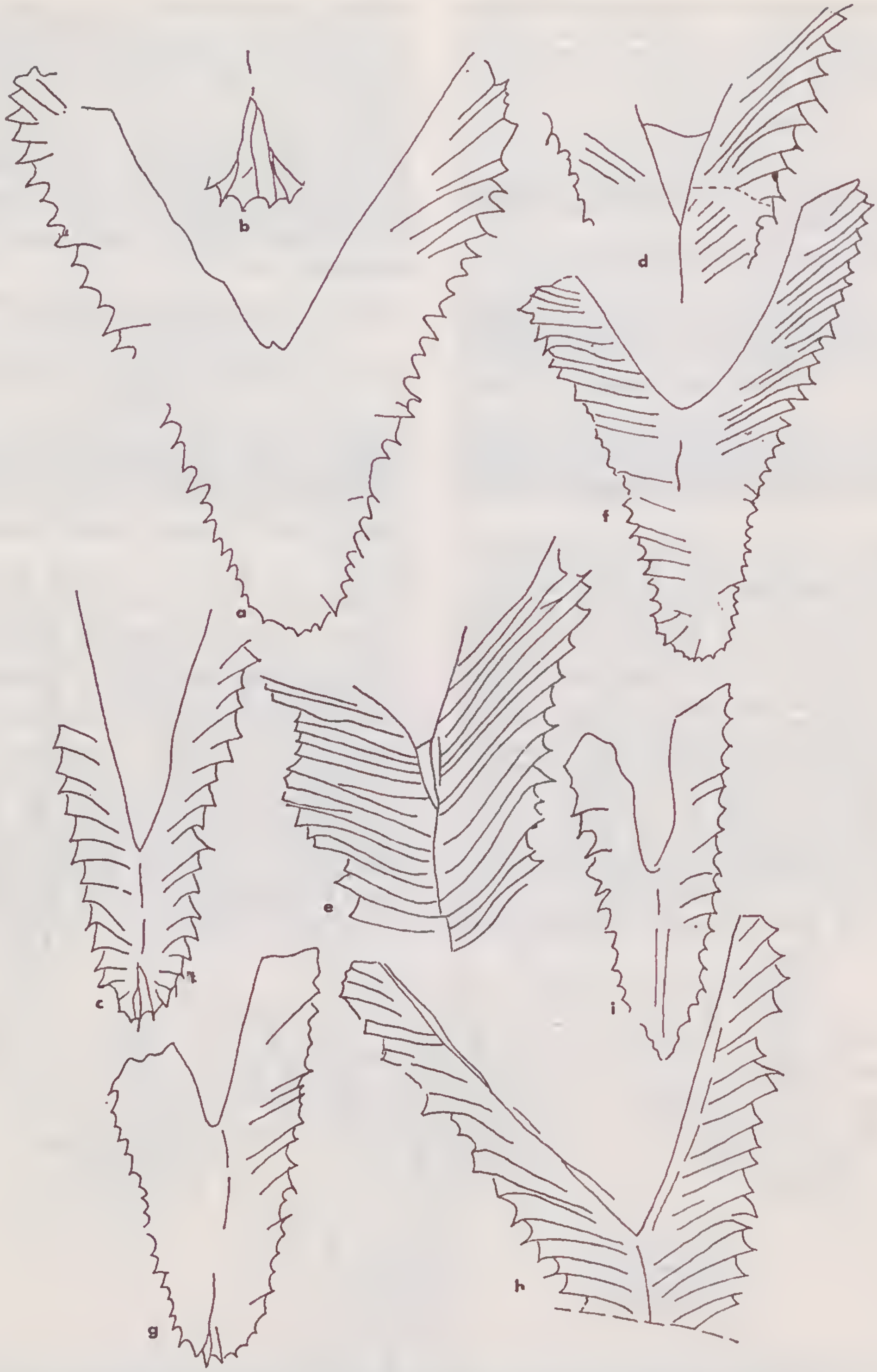


FIG. 14—*Oncograptus upsilon* (a) SM A22748 Loc. Ba71, Gisborne, × 3. (b) SM A 6325 Bullengarook Slate Quarry, Gisborne, × 3. *Oncograptus upsilon biangulatus* (c) SM A6333 Loc. Ba71, Gisborne, × 3. (d) SM A8140 Detail of bifurcation, El Paso, Texas, figured Bulman (1936), × 3. *Oncograptus upsilon* (e) GS 4079 Moorabool R. Bridge, Steiglitz-Meredith Rd. Detail of bifurcation, × 3. (f) GS 4080 Moorabool River, east from Meredith, × 1·75 approx. (g) GS 4081 Meredith Rd, Steiglitz, × 3. *Oncograptus upsilon biangulatus* (h) GS 4082 Little River, Brisbane Ranges, × 3. *Oncograptus upsilon* (i) GS 4083 Moorabool River, Steiglitz, × 3.

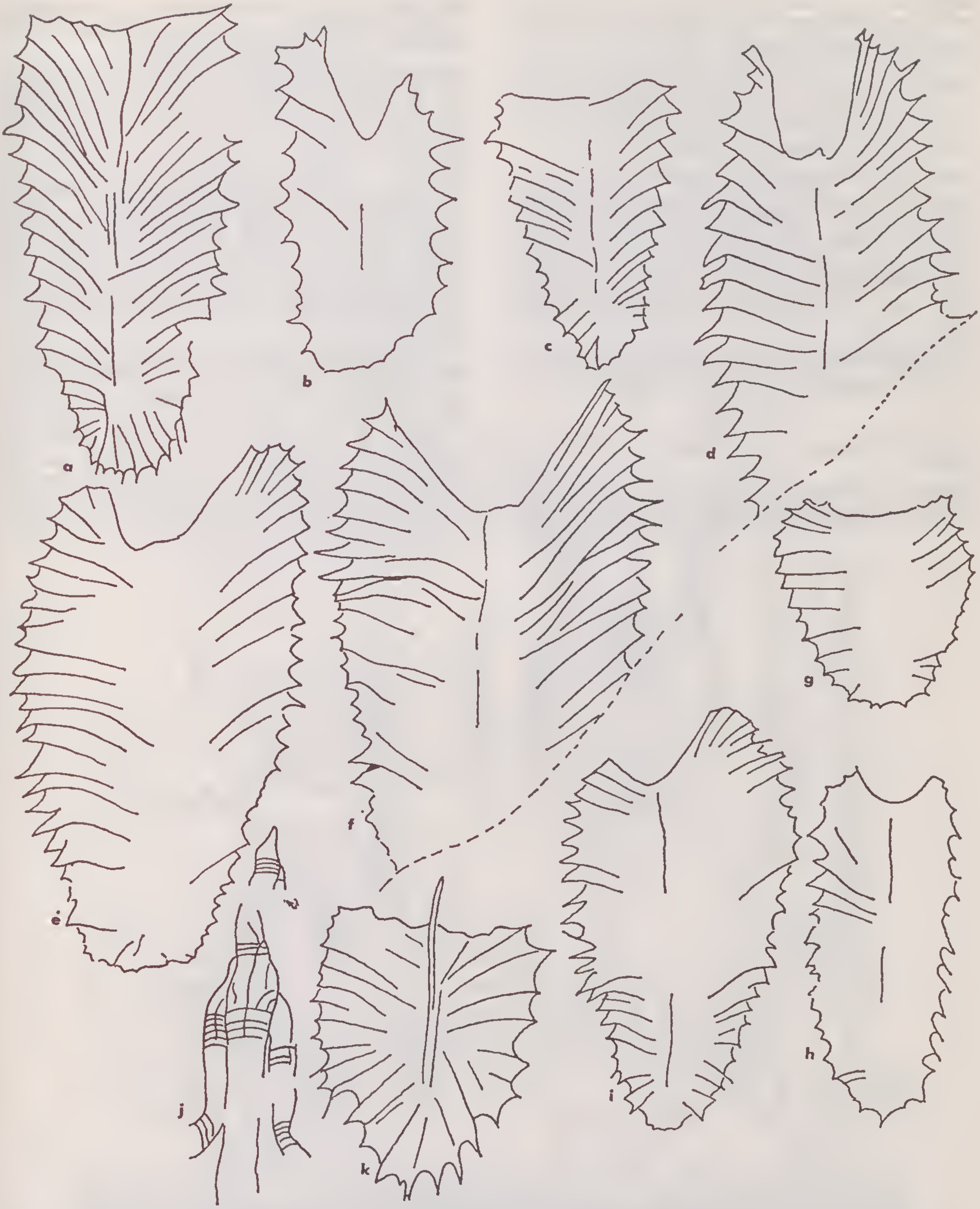


FIG. 15—*Cardiograptus morsus* (a) SM A6323c Chinamans Ck, Muckleford, × 3. (b) GS 4084 Moorabool River, Sheoaks, × 3. (c) GS 4085 Moorabool River, Sheoaks, × 3. (d) GS 4086 Anakie Gorge, × 3. (e) GS 4087 Same locality as (d), × 3. (f) GS 4088 Same locality as (d), × 3. (g) GS 4089 Same locality as (d), × 3. (h) GS 4090 Little River, Brisbane Ranges, × 3. (i) GS 4091 Moorabool River Bridge, Steiglitz-Meredith Rd, × 3. (j) GS 4092 Preserved on relief in pyrite. Sicular region. Coolebarghurk Ck, Sheoaks, × 6. *Cardiograptus crawfordi* (k) SM A60280 Strathfieldsaye, × 6.

with overlap complete. They number 12 to 13 in 10 mm. Apertural margins are concave, and well developed denticles are present.

The uniserial stipes have straight or slightly curved dorsal margins and diverge at 330°. The thecae are curved, but much less so than in the biserial portion. Thecae number 10 in 10 mm are 4 mm long, 0·8 to 1·0 mm wide, overlap 0·85 to 1·0.

Remarks: The length of the uniserial stipes does not appear to be significant and can vary considerably. The subspecies *O. upsilon biangulatus* H. and K. is always less than 1 cm wide at the bifurcation. The uniserial stipes have a greater angle of divergence (335° to 340°) and the uniserial stipes are always less than 5 mm wide. Thecae on the two forms are identical.

Genus **Cardiograptus** Harris and Keble 1916

Cardiograptus morsus H. and K.

(Fig. 15a-j)

1916 *Cardiograptus morsus* Harris and Keble in Harris

Material: Two specimens from Chewton, 17 specimens from Steiglitz and 1 specimen from Muckleford. One specimen from Steiglitz (Fig. 15j) preserved in pyrite, is the first example known which gives some indication of the proximal development.

Horizon and Localities: Zonal fossil of the Yapeenian Ya2. Range from the top of Ya1 to the top of Ya2. It is a short lived species. Recorded from Bendigo, Castlemaine, Gisborne, Steiglitz and Brisbane Ranges.

Description: Rhabdosome biserial throughout, up to 2 cm long and 3 mm wide proximally. The rhabdosome broadens to about 11 mm, at about ⅔ the length of the rhabdosome and then tapers to about 9 mm distally. In the narrow form of this species, the dimensions are length 8 to 9 mm, proximal width 2 mm, width at ⅔ length 4 mm, and width distally 3·5 mm.

Proximally, the thecae are strongly curved, but in distal thecae, curvature decreases. Apertural margins are straight to concave and denticles pronounced. The thecae number 10 in 10 mm with overlap 0·95.

Along the rhabdosome there is a progressive change in the direction of thecal growth: proximal thecae grow entirely downwards, but after the fifth, the thecae are horizontal and ultimately the south direction is upwards, so that distal thecae make a

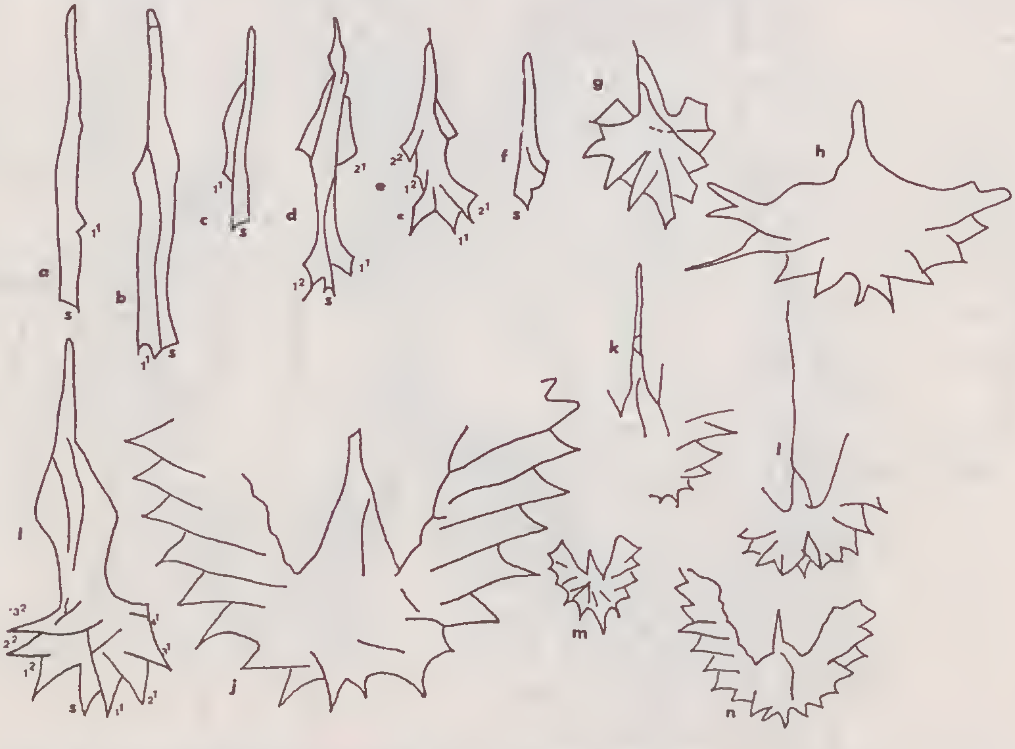


Fig. 16—*Pseudisograptus manubriatus.* All specimens from Wileys Quarry, Macedon. (a)-(i) Growth stages. SM A60281a, A60281b, A60281c, A60281e, A6351a, A6348a, A60281g, A60281a(i), A60282a, × 6. (j) Complete rhabdosome SM A6348b, × 6. (k) Proximal region SM A6327b, × 6. (l) Proximal region SM A6327b, × 6. (m) Small form SM A60284d × 3, figured Skevington (1968). (n) Normal form SM A60284b × 3, figured Skevington (1968).

sharp angle with the axis of the rhabdosome. Some specimens have a prominent virgula-like structure.

Cardiograptus crawfordi Harris

(Fig. 15k)

1926 *Cardiograptus crawfordi* Harris 1926

MATERIAL: Three specimens from Bendigo East. Preserved as purple films on pink slate.

HORIZON AND LOCALITIES: Darriwilian Da2 to Da3. Known only from Bendigo East.

DESCRIPTION: Rhabdosome biserial, 8 to 10 mm long and tapering from a width of 5 mm distally to 1·5 mm proximally. Thecae have concave apertural margins, with pronounced denticles directed downwards. Thecae number 11 to 13 in 10 mm, overlap 0·98 to 1·0. Proximal thecae pendent, and gradually direction of growth changes so that th8 is horizontal and subsequent thecae reclined.

REMARKS: The form is small, and is readily distinguished from *C. morsus*. The central virgula is particularly strong. Thecae are relatively shorter and broader than in *C. morsus*.

Family SINOGRAPTIDAE Mu 1957

Genus **Pseudisograptus** Beavis 1972

Pseudisograptus manubriatus (T. S. Hall)

(Fig. 16a-n, 17a-l)

1914 *Didymograptus caduceus* var. *manubriatus* T. S. Hall
1933 *Isograptus manubriatus* Harris
1968 *Maeandrograptus manubriatus* Skevington
1972 *Pseudisograptus manubriatus* Beavis

MATERIAL: Hall's type specimen is missing. The speciment of Hall Fig. 12 (T. S. Hall, 1914), nominated as lectotype by Harris (1933) by publication when the second syntype was removed to a new

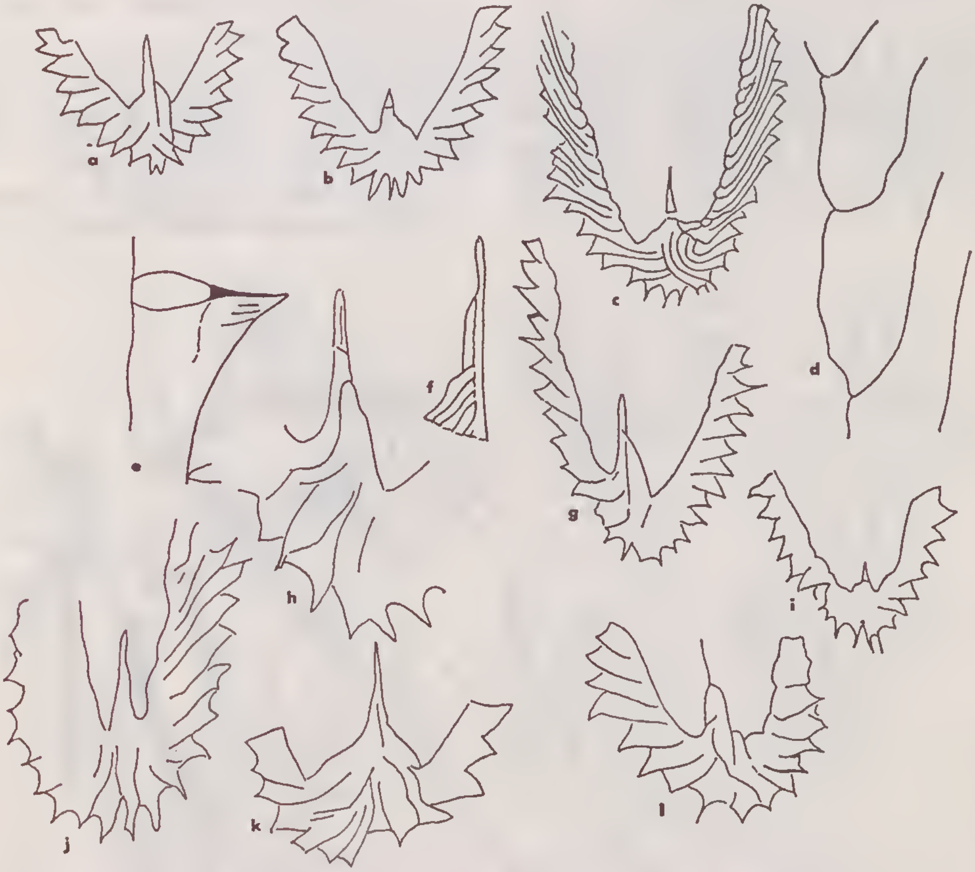


FIG. 17—*Pseudisograptus manubriatus* (a) SM A60284a, Wileys Quarry, Macedon, figured Skevington (1968), × 3. (b) SM A60284c Wileys Quarry, Macedon, figured Skevington (1968), × 3. (c) SM A603142 Marathon, Texas, figured Bulman (1968), × 3. (d) SM A603142 Marathon, Texas, showing prothecal folds, × 25. (e) SM A603142 showing thecal aperture, × 25. (f) SM A603142 showing apical portion of sicula, × 12·5. (g) GS 4093 Moorabool River, Sheoaks, × 3. (h) GS 4093 showing proximal region, × 6. (i) GS 4094 Moorabool River, Sheoaks, × 3. (j) GS 4095 Moorabool River, Shcoaks, small form, × 6. (k) GS 4096 Moorabool River, Sheoaks, × 6. (l) GS 4097 Steiglitz-Maude Rd, × 6.

species. The figured specimen of Harris (NV No. 13803) is imperfect; specimen SM No. A 6348b; and 72 examples from Wileys Quarry, Macedon, Victoria all preserved as film on black slate; 30 specimens, similarly preserved, from Steiglitz and specimen SM No. A603142 from Marathon, Texas, preserved in relief. In addition, uncatalogued material from Newfoundland, being studied by research students at Cambridge, was examined.

Horizon and Localities: Restricted to Yapeenian Ya1 and Ya2. The form has been recorded from Macedon, Gisborne, Castlemaine and Steiglitz.

Revised Diagnosis: Rhabdosome of two stipes diverging initially at 130° to 140°, but after the third theca on each stipe, at 300°. Initial thecae grow downwards and then curve outwards. Thecae long, with simple prothecal folds, imparting an undulate dorsal margin to the stipes. Initial thecae proliferate in the sicular region.

Description: The sicula is long: almost 1 cm in some specimens, but usually between 4 and 7 mm. It is narrow, with apertural width rarely exceeding 1 mm. The stipes are 1 cm long and about 3 mm wide. The dorsal walls are essentially straight, although in some examples there is a gentle curvature. In better preserved specimens, the dorsal wall is undulate (Fig. 16j, 17j) due to the simple prothecal folding. Proximally the thecae are 5 mm long, distally they are up to 7 mm long. Inclination of thecae decreases distally, e.g. th6^1 is inclined at 40° to the axis of the stipe while th10^1 is inclined at only 10° (specimen SM No. A 603142). Proximal thecae are strongly curved, distal thecae straight. Thecae number 10 in 10 mm, overlap 0·6. Denticles are pronounced. Apertural margins may be straight, concave or convex, are directed outwards in the proximal thecae, upwards in distal thecae.

Remarks: This species has been discussed in detail by the author in a recent publication (Beavis 1972). Reference should be made to that paper.

Pseudisograptus hastatus (Harris)

(Fig. 18a-g)

1914 *Didymograptus caduceus* var. *manubiatus* T. S. Hall
1933 *Isograptus hastatus* Harris
1972 *Pseudisograptus hastatus* Beavis

Material: Five specimens from Bagshot, near Bendigo, two specimens from the Castlemaine district, and three from Steiglitz.

Horizon and Localities: As Harris noted, the confusion with *P. manubriatus* has meant that many of the records are unreliable. It has a certain range from Ya1 to Da1. It has been collected from Yandoit, Castlemaine, Bagshot and Steiglitz.

Diagnosis: Small rhabdosome of two stipes diverging at a small angle initially, but distally at 330°. Stipes

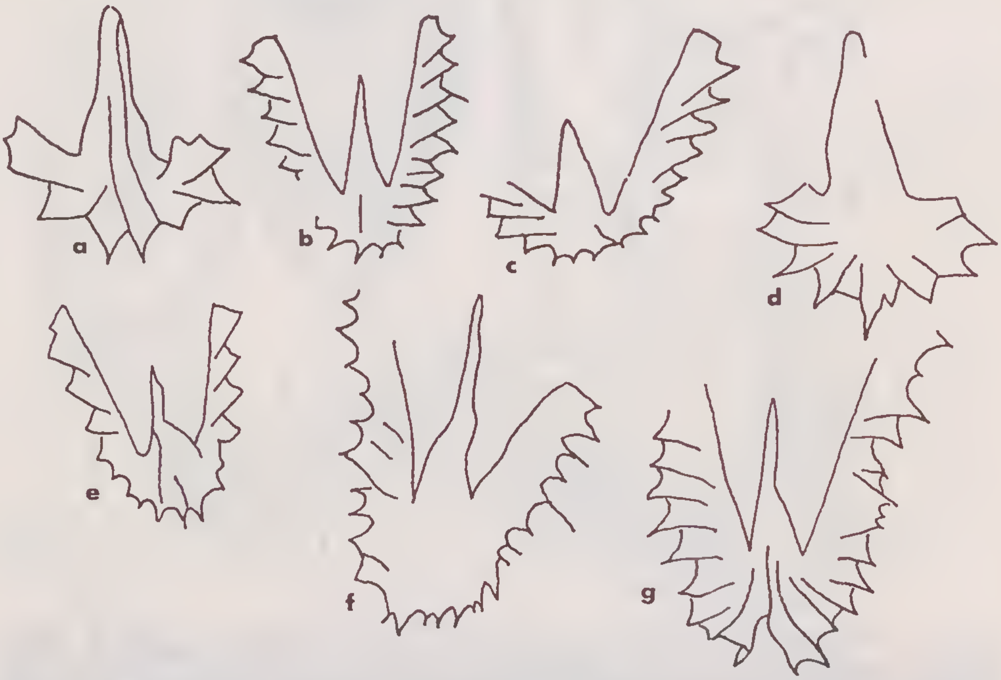


Fig. 18—*Pseudisograptus hastatus* (a) SM A6330 Juvenile form Limestone Ck, Yandoit, × 8. (b) SM A6332a Sandy Creek Rd, Bagshot, × 4. (c) SM A6332c Juvenile form, same locality as (b), × 8. (d) SM A6332b Same locality as (b), × 4. (e) SM A6331 McCrae Street, Castlemaine, × 4. (f) GS 4098 Moorabool River, Steiglitz, × 4. (g) GS 4099 Moorabool River, Steiglitz, × 4.

taper gradually. Sicula long and tapering. Thecae simple tubes.

Description: The sicula is long (5 mm) and narrow (1·2 mm at the aperture), but appears to be broader. Initial thecae originate in the sicular region and have a *manubriatus* growth pattern. Thecae number 10 to 12 in 10 mm, overlap 0·45 to 0·6, are about 1 mm long and 0·4 to 0·5 mm wide. The denticle is prominent. Thecal apertures are concave and make an angle of up to 140° with the stipe axis.

The stipes are about 1 cm long and taper from a width of 0·7 mm proximally to 0·5 mm distally. Dorsal walls are straight.

Remarks: T. S. Hall regarded this species as a variant of *P. manubriatus*; it is, however, quite a distinct form. The angle of divergence in *P. hastatus* is greater by some 30° and the thecae are smaller. The sicular region of the two forms is similar, but in *P. hastatus* the sicula itself is relatively longer and more sharply tapering, while, except for th1^1, the initial thecae probably arise lower down in the area. The mode of proximal development appears to be the same in the two forms, essentially, but we cannot understand Harris' opinion that this anticipates the maeandrograptid type of development since *Maeandrograptus* appears first significantly earlier in the sequence than *Pseudisograptus.*

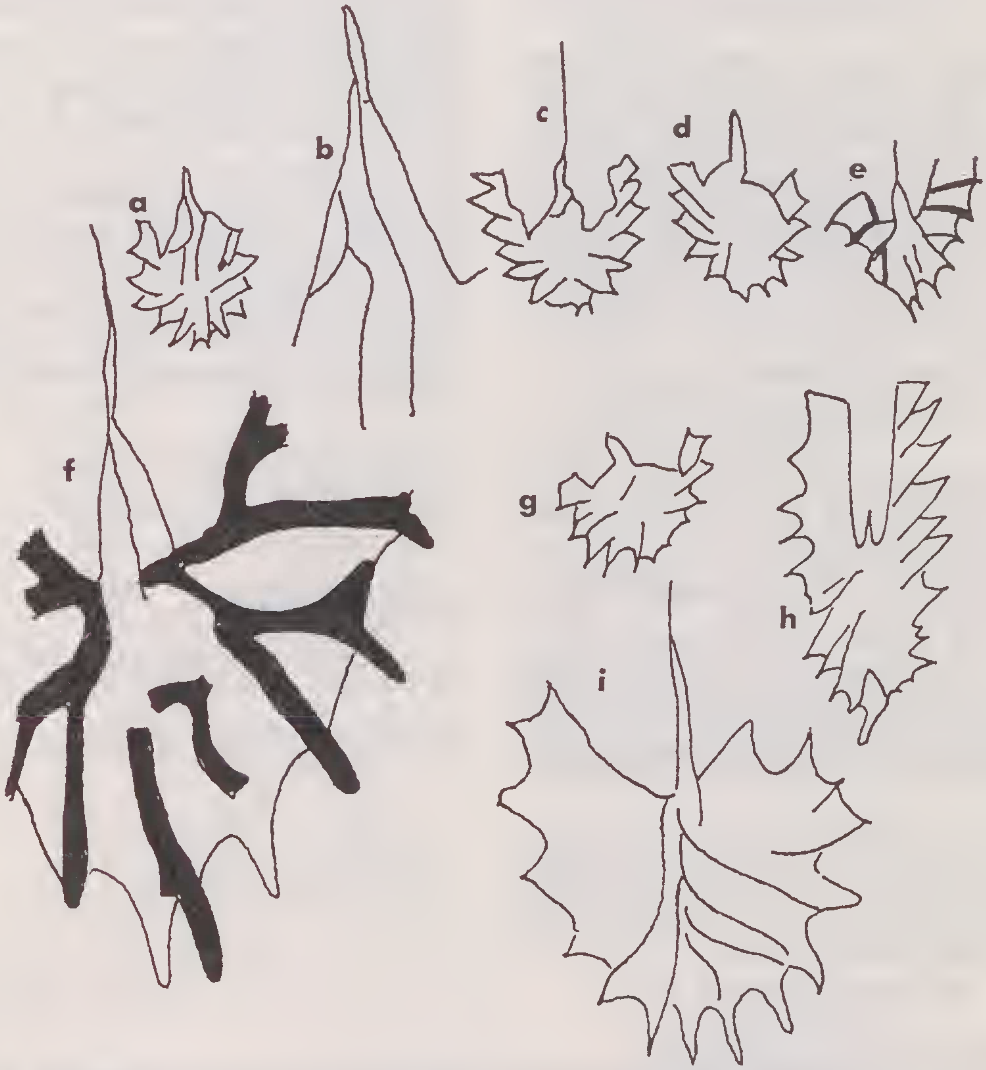


Fig. 19—*Pseudisograptus dumosus* (a) SM A22749 Locality Ba71, Gisborne, × 5. (b) SM A22749 Sicular region, × 21. (c) SM A6339 Lectotype, Loc. Ba71, Gisborne, × 5. (d) SM A6340a Loc. Ba71, Gisborne, × 5. (e) SM A6340b Loc. Ba71, Gisborne, × 5. (f) SM A6340b Proximal region, × 21. (g) SM A6336 Loc. Ba71, Gisborne, × 5. (h) GS 5000 Moorabool River, Sheoaks, × 5. (i) GS 5001 Little River, Brisbane Ranges, × 10.